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Performance Correlates of Social Behavior and
Organization in Non-Human Primates

Annual Report
Final Report

Bradford N. Bunnell

April 1982

Supported by

U.S. ARMY MEDICAL RESEARCH AND DEVELOPMENT COMMAND
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The purpose was to identify and investigate performance variables that
are correlated with social behavior and organization in non-human primates.
In two experiments, high ranking male rhesus monkeys (M. mulatta) working on
a fixed interval reinforcement schedule had lower baseline response rates
than animals that ranked low in their social groups. When reinforcement was
randomly omitted, the high ranking animals exhibited more response bursting
than the low ranking males.

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Subsequently, 23 male M. fascicularis (cynomologous, or crab-eating macaques) from three social groups were tested on a number of operant schedules, complex learning problems, and open field tasks. Levels of aggression were correlated with response bursting on a DRL schedule. High social rank was correlated with fast acquisition on DRL and changeover ratio schedules, poor performance on reversal learning set tasks, and increased response bursting following omission of reinforcement on a variable interval schedule. Relationships between social variables and open field exploration and response to novel objects were inconsistent or absent.

A concept of social stress was invoked to account for the relationships between social and performance variables that were demonstrated in the project.

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FOREWORD

In conducting the research described in this report, the investigator(s)
adhered to the "Guide for the Care and Use of Laboratory Animals," prepared
by the Committee on Care and Use of Laboratory Animals of the Institute of
Laboratory Animal Resources, National Research Council (DHEW Publication
No. (NIH) 78-23, Revised 1978).

Summary, Abstract, or Digest

The purpose of this project was to identify and investigate performance variables that are correlated with social rank, social behavior, and social organization in monkeys of the genus Macaca.

Two studies were conducted with male rhesus monkeys (M. mulatta) in which it was shown that in male rhesus monkeys working on a fixed interval (FI) schedule, high ranking animals in the social dominance hierarchy had lower baseline response rates than low ranking males. When reinforcement was omitted following 20% of the FI schedule intervals, the high ranking animals showed more response bursting than did the low ranking animals.

Attempts to replicate the rhesus monkey studies using males from two breeding troops of crab-eating macaques (M. fascicularis) produced equivocal results. The fascicularis tended to deal with the contingencies of the FI schedule differently than did the rhesus in that high baseline responding was related to high rank and response bursting following omission of reinforcement was positively correlated with baseline response levels in the majority of animals. Perhaps because of this, the performance changes which occurred following experimental manipulations of the social structure of the troop were not consistent with changes in social behavior and status.

Two further studies investigated the effects of the omission of reinforcement on performance on a random interval schedule. Using a paradigm designed to assess "frustration" following omission of reward, it was found that high rates of response bursting were correlated with high rank in one of the fascicularis troops, but not the other. Because there was much more agonistic activity in the former troop than the latter, it was hypothesized that the relationship between performance and social variables might be present only when the group structure was under tension produced by factors which tended to increase aggression. In the second study, a new troop was formed, using some of the males from the two original troops. During the formation of the troop and the establishment of dominance relationships between individuals, strong relationships between response bursting and social rank appeared. A year after the second study, the animals in the new troop were retrained on the random interval schedule. Although response bursting was lower in all of the animals following the introduction of the omission of reward condition, a significant relationship between high rank and bursting was still present.

Fascicularis were also trained and tested on a differential reinforcement of low rate (DRL) to which a limited hold requirement had been added. In general, high ranking monkeys were better in acquiring efficient performance on this task than low ranking animals. Response bursting following a failure to delay a response long enough to meet schedule requirements was correlated primarily with frequency of aggressive responses within the troop and secondarily with social rank in the dominance hierarchy. This experiment was also replicated and the results confirmed the earlier findings.

Good performance on the acquisition of a changeover ratio task which required an animal to make 12 lever presses before making the response which resulted in reward was correlated with high social status in fascicularis males. Performance after the task had been learned was not related to any social variables, however.

High ranking animals did worse than low ranking animals on a visual discrimination reversal task and object quality learning set reversal problems. This did not appear to be a function of their ability to acquire the concepts involved, but probably reflected difficulty in responding to a sudden change in the contingencies and requirements of the task at hand.

Although there was a tendency for high ranking animals to enter an open field and engage in more locomotor activity upon first exposure to the field than low ranking animals, the relationship was not very strong and disappeared with repeated exposures. No relationships between social variables and responses to novel objects placed in the field were found. Exposing animals to other animals, both familiar and strange, in the open field did not produce any information that was not obtainable from observing the same animals in the troop situation.

Extensive study of the social behavior of the two breeding troops of fascicularis revealed the general contributions of affiliative behaviors and of matriarchical groups to the social organization of the troops. However, it was concluded that the role of these factors was secondary to intermale agonistic behavior in structuring and maintaining the adult male social dominance hierarchy.

Overall, the performance of subadult males on operant schedules and on complex problem solving tasks was consistently better than that of the adult males. These animals, which interacted primarily with juveniles and with other subadults, were not heavily involved with the establishment or maintenance of the adult male hierarchy.

A concept of social stress was invoked to account for the relationships between social and performance variables that were uncovered in this project.

Body of the Report

This project utilized an animal model to identify and investigate relationships between social behavior and performance. Because members of social species spend a great amount of time and effort interacting with the other members of their societies, it might be expected that such interactions, and their consequences, would have pervasive effects on individual behavior. Such effects might modulate the way in which individuals perform on tasks that are important for the individual or for the group to which the individual belongs. If this were the case, then an understanding of the nature of the relationship between performance variables and social variables would have important implications for the prediction and control of performance.

In this project, nonhuman primates from two highly social species of macaque monkeys were tested on performance on a number of standard laboratory tasks. Attempts were made to relate individual performance to the social behavior and social status of each subject and to modify performance by manipulating the social environment of the animals. The use of an animal model allowed good control of the experimental conditions over an extended period of time and made possible extensive manipulations of the social behavior and social status of the subjects.

The first objective was to determine whether or not relationships between performance and social behavior could be demonstrated in nonhuman primates. Once this had been accomplished, we began the task of trying to understand the nature of such relationships in terms of their reliability relative strength, and direction or proximal cause. With respect to causation, we recognized three factors which, separately or in combination, might account for correlations between performance variables and social variables:

First, there might be a trait, or constellation of traits, which would predispose a particular individual to both a certain kind of social behavior and to a certain kind of performance. For example, good visual acuity might contribute both to a monkey's performance on a visual discrimination problem and to its ability to detect visual signals that are important social stimuli. In this instance, a relationship between social behavior and performance would be attributable to the relative importance of a particular trait, or traits, in each class of behavior and to the degree to which such traits are present in different individuals in the social group.

Second, the emotional or other consequences of an individual's good or poor performance might be transferred or displaced to other situations and affect social behavior. For example, a person frustrated by the inability to complete a task might be aggressive or sullen towards family or coworkers, producing a subsequent deterioration in social relationships. On the other hand, improved social relationships might result from an individual's sharing of the emotional or monetary rewards for a job well done with others.

A third possibility is that the effects of social encounters and social relationships might carry over to the task situation and affect performance. This is a reversal of the causal sequence suggested in the preceding paragraph. A monkey that has established itself as the alpha male in a troop might approach a test involving presentation of novel stimuli with boldness and confidence and perform with short latency responses, whereas an animal that

has recently lost social status might be hesitant and slow in responding to the same stimuli. In humans, it might be expected that performance on group oriented tasks would be poorer in groups where divisive or unresolved social relationships exist than in groups that are well integrated and exhibit little internal friction. Whether the degree of stability of intragroup relationships might also be expected to affect individually oriented performance is less certain, but it opens an interesting and potentially important question.

Prior to the present project, there had been very few attempts to relate learning and performance, as defined by laboratory paradigms, to social status, social organization, and the dynamics of social behavior as revealed by observations of behavior in groups of monkeys. Meier and Bartlett (Meier, 1971; Bartlett & Meier, 1971) examined operant behavior in a communal group of rhesus monkeys (M. mulatta). In these studies, the manipulandum for the task (a lever) was present in the cage with the group. The results showed that dominant animals had precedence at the manipulandum, responded at relatively low rates, and paused to eat the food reward after it was delivered. Subordinate animals did not respond in the presence of higher ranking animals, they responded at high rates, and they often resumed lever pressing while eating a recently delivered piece of fruit. Individual differences in the rate or intensity of responding did not vary as a function of social context, suggesting that the individual differences in performance were quite stable. The authors felt that the differences might be due to a past history of differential learning of dominance related behaviors. Since performance was observed while the animals were in the group situation, these studies did not provide evidence that individual differences in learning and performance are related to social status when no other animals are present in the testing situation.

We know that social organization places certain constraints on the individual behavior of group members. A demonstration that individual differences in learning and performance of animals behaving in isolation from other group members bear a relationship to the dynamics of the organization of the social group would be an important initial step toward an understanding of how social relationships advance or restrict the expression of individual potential. Conversely, the expression of individual potential as revealed by the ability to master certain laboratory tasks might prove to be of value in understanding the ways in which an individual monkey is more or less suited to a particular role within its social group. Such information can be of considerable importance to our attempts to understand primate social behavior and organization.

Strayer (1976) studied the relationship between imitational learning and social status in subadult male pigtail monkeys (M. nemestrina). While this research did not provide evidence for "true" imitation in these animals, it did reveal learning and performance differences that were related to social parameters. A cued alternation problem was given to high and low ranking animals and it was found that the high ranking monkeys made significantly more total responses during each test session than low ranking animals. The high status animals also made more time-out errors. Overall, the high status monkeys were less likely to withold responses during the tests, this operated against them in the sense that good response inhibition was important

for mastering this experimental task. Strayer felt that differences in social learning between dominant and subordinate monkeys could account for these results. According to this interpretation, performance on the problem relected individual differences in adaptation to group living conditions. Thus, lower ranking animals are continuously exposed to aversive social control which requires that they inhibit certain specific responses whereas dominant animals are rarely required to do so. Alternatively, genetically or ontogenetically based differences in response inhibition could affect both social status and performance on the laboratory task.

Our first study involved examined the performance of rhesus monkeys on an operant task that included a condition under which reinforcement was omitted:

Social Rank and Omission of Reinforcement in Rhesus Monkeys (M. mulatta).

In this experiment, the performance of 22 adult male rhesus on a Fixed Interval 1-min reinforcement schedule was examined under conditions where the reinforcement probabilities were either 1.00 or .80. The results were then correlated with the social rank of the animals at the time they were taken from their social groups for testing (Bunnell, Kenshalo, Allen, Manning & Sodetz, 1979a).

The animals were obtained from the Lawrenceville Field Station of the Yerkes Regional Primate Research Center. Eighteen came from an all male group that originally consisted of 24 animals when it was established in the winter of 1969-70. Four came from a group of nine males and six females whose members had been reared under various conditions of social deprivation. The animals were brought to the laboratory, usually in squads of four, and individually housed in the operant testing chambers throughout training and testing. Data on the social status of each animal was provided by Yerkes personnel who had the social groups under observation throughout the course of the study. During the two years or so it took to complete the study, changes took place in the size and composition of the groups from which we received our subjects and experimental manipulations of the dominance relationships were undertaken by the Yerkes scientists. The social status of each of our subjects was always taken to be his rank at the time he was removed from the group, regardless of the makeup of the group at that time.

The animals were trained to press a lever for food reward (banana pellets) and placed on a fixed interval 1-min (FI 1-min) reinforcement schedule. The animals were given two sessions a day and allowed to earn 70 pellets during each session. Water was available _ad libitum_ and intake was monitored with a drinkometer circuit.[1]

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[1] During much of this time, studies of schedule-induced polydipsia, were part of the contract research but were dropped when the mission of the division of Neuropsychiatry of WRAIR was changed. A list of reports and papers from this work is included in the Bibliography of the Project.

On the FI 1-min schedule a reinforcer is delivered upon the occurrence of the first lever press following a 1-min interval after the last reinforcer was received. As training progresses, responding tends to become concentrated toward the end of the 1-min interval. In well trained animals, a plot of responses within an interval yields a "scalloped" curve in which response frequency is very low right after a reinforcer is received and increases rapidly at the end of the interval. The magnitude of the scallop effect can be assessed by computing an "Index of Curvature" (IC) which reflects the extent and direction of the difference between the cumulative response curve actually produced by the animal and a straight line which would be produced by a constant rate of responding (Fry, Kelleher & Cook, 1960). Our animals were trained until they achieved a criterion of an IC of at least +.40 each day for 14 consecutive days.[2] During training, 100% of the 1-min intervals were reinforced, i.e., the animal always received a banana pellet when it met the schedule requirements. Once the training criterion had been met, the animals were shifted to a reinforcement probability of .80. On this schedule, only a randomly determined 80% of the intervals were reinforced. Although the animals now did not receive a banana pellet 20% of times they would have received one under the 100% schedule, they were still allowed to earn 70 pellets per test session. The .80 probability of reinforcement schedule was presented for a minimum of 10 days (20 test sessions). Additional procedural details are available in the published report of this experiment (Bunnell, et al, 1979a).

When a food pellet is not delivered when an animal presses the lever at the end of a 1-min interval, the subject usually produces a burst of responses which occur at the beginning of the next 1-min interval. The typical scalloped response curve tends to break down with a concomitant depression of the index of curvature (IC). A measure of this effect is obtained by computing the ratio of nonreinforced to reinforced responses per interval. A ratio greater than 1.00 indicates a greater response frequency after omission of the delivery of the food reward and can be used as a measure of response bursting. A number of authors (see McMillan, 1971) have called attention to the similarities between this response bursting and the increased vigor of response seen in the double runway situation used to study frustrative nonreward (e.g., Amsel, 1958). However, Staddon and his coworkers (e.g., Staddon & Innes, 1969) prefer the term "omission effect" to "frustration effect" to describe the effects of omission of reinforcement on operant performance. They argue that the effect can be accounted for in terms of the discriminative effect of reinforcement and that a motivational interpretation involving the energizing effects of frustration is unnecessary. Accordingly, we have adopted the term "reinforcement omission ratio" (R_o) for the ratio of nonreinforced to reinforced responses as it is a more neutral term than the alternative expression, "frustration ratio".

The performance of animals whose social rank placed them in top half of their groups (n=11) was compared with that of those which were ranked in the bottom half of their groups (n=11) at the time they were brought to the laboratory for testing. The results may be summarized as follows:

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[2] With the 1-min fixed intervals divided into four 15-sec time bins, the value of the IC can range from +.75 (all responses in the last 15 sec before the end of the interval) to -.75 (all responses in the first 15 sec of the interval). An IC of 0.00 would indicate that the responses were evenly distributed across all four 15-sec bins.

1. The mean number of testing sessions required in reaching the IC criterion of +.40 was 14.2 for the high ranking animals and 18.1 for the low ranking animals. The difference between the means was not statistically significant. Thus, there was no evidence of a difference between high and low status animal in the acquisition of criterion performance on the FI-1 min schedule.

2. Performance data obtained prior to and after the reinforcement probability (P_r) was shifted from 1.00 to .80 are given in Table 1. The mean number of responses per reinforcement for the last 20 test sessions prior to the shift in reinforcement probability is given in the third column of Table 1. On the basis of the work of Bartlett and Meier (1971) we predicted that the higher ranking set of animals would have lower response rates than the low ranking animals. This proved to be the case as the high ranking animals made only about half as many responses per reinforcement than the low ranking animals (t = 1.91, df 20, p <.05, one-tailed test). The four animals that were reared in social isolation all had very low response rates. Excluding them from the analysis reduced the variability of our samples and made the differences more apparent (mean high rank = 9.5, low rank = 18.3, t = 2.27, df 16, p <.02, one-tailed).

3. The fourth column of Table 1 gives the correlations between responses per interval following a reinforcement and response per interval following nonreinforcement for each animal. In 18 of the 22 animals, there were high, positive, statistically significant correlations between the two measures (p <.05, two tailed) indicating that high rates of response following reinforcement were associated with high rates of response following nonreinforcement and vice versa in these animals. Three of the animals had low, nonsignificant correlations and one had a high, negative correlation. These four animals dealt with the contingencies of the schedule in a qualitatively different way than the other 18 that were tested.

4. The fifth and sixth columns of the table give the ICs for reinforced (col. 5) and nonreinforced (col. 6) intervals. There were no difference in performance between the two groups and the ICs of both high and low status animals were equally dis of reinforcement.

5. The last column of the table gives the median omission ratios (R_o) for all sessions where the probability of reinforcement (P_r) was .80. The mean of the medians for the high status group was 4.48; for the low status animals it was 3.10. The difference between the means was not significant (t = 1.81, df 20, p = .085, two-tailed). However, excluding the four animals which did not exhibit a high positive correlation between reinforced and non-reinforced response rates (see section 3 above) gave means of 4.46 for the high status group and 2.57 for the low status group. The difference between the means was significant (t = 2.46, df 16, p <.03, two-tailed). Thus, in this subset of animals, high status animals had higher R_os than low status animals.

Table 1

Social Rank and Operant Performance of 22 Adult Male Rhesus Monkeys

Animal	Rank in Group	Responses per Reinf.	r: Reinf. to Nonreinf. Responses	Index of Curvature Reinforced	Index of Curvature Nonreinforced	Median Omission Ratio
HIGH STATUS ANIMALS:						
Wink	1/15	5.41	.60	.63	.22	3.36
Marbles	2/15	7.65	.50	.56	.10	5.89
Iman	2.5/19	16.76	.88	.53	.24	3.36
Ernie	2.5/19	14.22	.56	.63	.10	3.27
Ancient	8/34	10.44	.81	.50	-.01	2.15
Nick	10.5/34	8.12	.57	.68	.28	2.61
Fakir	8/20	10.38	.67	.71	.20	6.50
Gallant	8/20	5.93	.76	.66	.27	4.07
Inspector*	3/7	7.55	.74	.71	-.05	7.31
Kant**	1/15	2.97	-.22	.63	.13	4.72
Nipsy	2/15	3.82	.51	.66	.40	6.07
		X̄= 8.48		X̄= .63	X̄= .16	X̄= 4.48
LOW STATUS ANIMALS:						
Herman	11/19	7.57	-.47	.64	.15	3.37
Drogue	19.5/34	37.42	.84	.37	.13	2.09
Tonto	25.5/34	12.95	.72	.57	.09	2.27
Vulcan	15/19	24.93	.50	.65	.19	3.81
Kelley	16/20	30.01	.88	.18	.02	1.26
Keeper	16/19	2.45	-.06	.60	-.14	2.64
Editor*	20/20	17.91	.81	.60	.15	2.31
Arctic*	6/7	14.52	.90	.44	.15	1.94
Hercules**	7/7	16.73	-.07	.66	.17	7.53
O'Rourke**	12/15	2.75	.80	.65	.31	1.59
Zorro	15/15	3.80	.54	.70	.20	5.28
		X̄=15.54		X̄= .55	X̄= .13	X̄= 3.10

* Taken from all male subgroup of seven animals that were originally part of the larger group of 34 males.
** Taken from a group of 15 (9 males and 6 females) monkeys reared under varying conditions of social isolation.

This study produced two potentially important findings. First, the data indicate that high ranking animals tend to respond on an operant schedule at lower rates than low status animals. This confirms and extends the Bartlett & Meier (1971) results to a different schedule of reinforcement and to a situation where the animals are performing in isolation as opposed to a group situation. Bartlett and Meier suggested that status related differences in performance might be the quite stable resultants of a history of differential learning of dominance related behaviors. Our results suggested that the differences in response rates were indeed persistent, since they were maintained for periods of up to six months after the animals were removed from their peer groups.

Although there were no differences between the high and low status groups in the acquisition of criterion performance on the FI-1 min schedule, the performance of the high status animals was more efficient in the sense that they expended fewer responses for each reinforcement received under the $P_r =$ 1.00 reinforcement contigency. This keeps open the possibility that there may be factors which predispose an animal to both efficient performance and high rank.

The second finding of interest was the tendency toward higher omission ratios in the high ranking set of animals. This was quite clear in the 18 animals who exhibited high positive correlations between response rates after reinforcement and rates after omission of reinforcement. The high positive correlations suggest that the larger R_0s exhibited by the more dominant animals was due to a relatively greater increase in responding after nonreinforcement than was the case for the lower ranking animals.

Thus, the greater response bursting by high ranking monkeys could not be explained solely in terms of their lower baseline response rates and appeared to be a real and independent effect. Once again, two possible explanations for the result were available. One was Strayer's (1976) hypothesis, mentioned earlier, that involved a concept of differential social learning which led to increased response inhibition in subordinate animals. The other, that genetically or ontogenetically based individual differences in response inhibition that affected both social status and performance on the laboratory task.

Social Group Formation and Operant Performance in Rhesus Monkeys

There were some individual exceptions to the general trends obtained in the results of the first rhesus monkey study described above. Animals that had been reared under varying conditions of social deprivation tended to have very low baseline response rates on the operant task. Four of the 22 animals in the study did not exhibit the high, positive correlations between response rates after reinforced and nonreinforced intervals that were typical of the other 18 subjects. Another concern was the lack of contiguity between the social data and the tests of performance in the laboratory. The monkeys were removed from their social groups and taken to the laboratory where they remained throughout training and testing on the laboratory task. When, after laboratory testing was completed, they were reintroduced into social groups, they invariably underwent a change in social status. To examine the robustness of the results from the first experiment and to provide contiguity

between the social data and laboratory performance a second experiment was undertaken.

Adult male rhesus monkeys were again tested on a FI 1-min schedule of reinforcement with Pr = 1.00 or .80, but this time observations of social behavior were made daily so that day-to-day changes in both performance and social interactions could be ascertained. In addition, the social situation was experimentally manipulated by introducing new animals to the group and monitoring concurrent changes in performance.

Six adult male rhesus monkeys were obtained from the Yerkes Field Station in Lawrenceville. They had been members of the same all male group of 34 animals from which the majority of the monkeys in the first study had come. Two animals were removed from the social group in May, 1973, the other four were removed in September, 1973. During initial training and testing, the animals were housed in individual cages in an airconditioned colony room adjacent to the room which contained the operant conditioning chambers. The diet consisted on the banana pellets received during the test sessions, sup- plemented by fruit and vitamins. During and after social group formation, the animals were housed in an outdoor compound with a concrete floor and walls and roof made of 2" mesh chain link fencing. The compound measured 12.2x3. 4x2.0 m high and was connected to a heated and airconditioned indoor cage 6.1x1.2x2.5 m high by an enclosed runway 1.3 m wide and 1.3 m high. Metal perches were located in both the compound and the indoor cage as were drinking fountains. An observation station 1.5x1.6x2.0 m high was centrally situated within the compound. Six operant chambers were available for testing the animals; a portable tape recorded was used to record social observations. Data from the tapes were punched onto paper tape and analyzed with the aid of a PDP-8E laboratory computer.

The monkeys were trained and tested on the FI 1-min schedule according to the same procedures used in the first experiment. Prior to social group formation, the animals received various combinations of tests with the Pr = to either 1.00 or .80. Two of the animals were also used on a study involving a range of fixed interval schedules (see Kenshalo and Allen, 1976). When the group was formed in August, 1974, two of the animals, Tonto and Loki had been out of social contact with other monkeys for 14 months; the other four, Jason, Kansas, Pardner, and Zeus, had been removed from social contact for 11 months.

During and after group formation, social behavior data were obtained, using the behavior inventory given in Table 2. The group was observed for 1 hr, twice a day, weather permitting, immediately after the animals completed the morning and afternoon operant testing schedules. Trained observers were used to record the behavior of each animal as it occurred, noting the initiator of the behavior, the behavior itself, and the recipient, if any, of that behavior. Either one or two observers were present for each observation period. Social rank was determined by defeats. The occurrence in any animal was subordinate to the monkey toward which the signal was directed. With the aid of the laboratory computer, response matrices for each animal with respect to every other animal in the group were constructed for both aggressive and submissive classes of behavior. The submission matrices were used to determine the dominance hierarchy.

Table 2

Functional Categories of Behavior Used in Recording

Observations of Male Rhesus Interations

<u>AGONISTIC</u>

Aggressive:

Threat (open mouth)
Charge
Slap
Nip (bites with incisors only)
Bite (uses canines)

Submissive:

Avoid
Grimace (open mouth, teeth exposed, no vocalization)
Squeal (grimace plus vocalization)
Flee

Other:

Demonstration
Enlist

<u>NONAGONISTIC SOCIAL</u>

Present to groom
Allogroom
Move (in company with one or more animals)
Sexual Present
Mount (no thrusting)
Mount (with thrusting)

<u>NONSOCIAL</u>

Sit (separated from others by 1 m or more)
Self groom
Masturbate

Group formation was initiated on August 25, 1974 by releasing Kansas, Pardner, Loki, and Zeus into the compound. Zeus was severly bitten and had to be removed from the group for treatment of his injuries. Jason was introduced to the group on September 10, 1974 and Tonto followed on September 23. A second, and successful attempt to put Zeus into the group took place on October 7, 1974. Operant testing and social observations continued through November 20, 1974 when the animals were returned to Yerkes. Additional procedural details may be found in the published report of this experiment (Bunnell, Kenshalo, Czerny, & Allen, 1979b).

Summaries of all of the agonistic interactions among the animals have been published (Bunnell, et al, 1979b). A sample of the agonistic response matrices is given in Table 3 which summarizes the aggressive and submissive interactions during and following Tonto's introduction into the group. The matrices on the left side (Table 3a) were derived from the dyadic interactions observed during the 1-hr observation period immediately following Tonto's introduction on September 23, 1974. The matrices on the right give the same information for all of the observations (15) made between September 24 and October 6. (Another animal was put into the group on October 7). Only clearly aggressive and submissive behaviors were used in constructing the matrices. The frequency of behaviors in the categories threat, charge, slap, nip and bite (see Table 2) were combined and used for the aggression matrixes; avoid, grimace, squeal and flee were the categories used in the submission matrices. In reading the matrices, the instigators of the behavior are listed in the column to the left, the recipients in the row across the top. Thus, during the introduction, Tonto directed 5 aggressive behaviors toward Loki, 5 toward Kansas, none toward Pardner, and 1 toward Jason. He was subjected to aggressive behavior from Loki 31 times, from Kansas 17 times, etc. Tonto submitted 40 times to Loki, 28 times to Kansas 3 times and Pardner and 35 times to Jason. During this time, Loki did not submit to any other animal, Kansas submitted only to Loki, and so on down the line.

Throughout the study, the dominance structure in the group was linear and unambiguous. As each new monkey was introduced, it was attacked by the other animals, easily defeated, and became the lowest ranking member of the group. After the initial flurry of aggression that accompanied each introduction, aggression fell to a low level and remained so until another new animal was introduced. There were no reversals in rank during the study.

The number of operant testing sessions required by each monkey to reach a criterion of 28 consecutive sessions with an IC of +.40 or better was obtained. (The 28 criterion sessions were not included in this score.) The response rates (number of responses per reinforcement) were calculated for both the criterion sessions and for the last 20 sessions prior to switching the monkeys to a reinforcement probability of .80. These data, together with the social rank of each animal at the time it was removed from its Yerkes group and the relative rank of each animal with respect to the others are presented in Table 4. As in the previous study, there was no relationship between trials to criterion and previous social rank. With the exception of Tonto, the response rates of the monkeys during the IC criterion sessions were related to the pretesting social rank. Tonto, a very low ranked animal, had served as a subject in the first experiment and had a high response rate (12.95) at that time. Perhaps extensive experience with the schedule contingencies produced the change in performance. Indeed, two other shifts in per-

Table 3

Frequency of Aggressive and Submissive Responses Directed by Each Monkey
Toward Other Group Members During and Following Tonto's Introduction.

a. Tonto's Introduction 9/23/74:   b. 9/24 - 10/6/74 (15 observations):

Aggression:

	LOKI	KANSAS	PARDNER	JASON	TONTO
LOKI	–	0	0	0	31
KANSAS	0	–	0	0	17
PARDNER	0	0	–	1	3
JASON	0	0	0	–	19
TONTO	5	5	0	1	–

	LOKI	KANSAS	PARDNER	JASON	TONTO
L	–	1	0	0	0
K	0	–	0	0	0
P	0	0	–	0	8
J	0	0	0	–	8
T	0	0	0	1	–

Submission:

	L	K	P	J	T
LOKI	–	0	0	0	0
KANSAS	3	–	0	0	0
PARDNER	1	0	–	0	0
JASON	7	2	3	–	0
TONTO	40	28	3	35	–

	L	K	P	J	T
L	–	0	0	0	0
K	11	–	0	0	0
P	1	1	–	0	0
J	16	6	42	–	0
T	12	3	42	35	–

Table 4

Previous Social Rank, Trials to Index of Curvature (IC) Criterion of +.40, and Response Rates
on FI 1-min Schedule with Reinforcement p = 1.00 for Six Male Rhesus Monkeys

ANIMAL	PREVIOUS RANK AT FIELD STATION	RELATIVE RANK	TRIALS TO CRIT.	RESPONSE RATES FOR: IC CRITERION TRIALS	LAST 20 TRIALS p = 1.00
LOKI	T 5/18	1	63	4.10	4.33
ZEUS	4/12	2	52	4.50	4.14
JASON	5/12	3	58	6.65	9.58
PARDNER	6/12	4	100+	11.18	12.27
KANSAS	10/12	5	18	10.50	3.38
TONTO	17/18	6	0*	1.85	2.05

*Tonto was tested previously in the Winter of 1972. At that time his response rate was 12.95
responses/reinforcement on the FI 1-min schedule.

formance occurred prior to the time the animals were placed on a reinforcement probability of .80. Kansas, a low ranking animal with a high rate of response on criterion trials (Table 4, col 4) exhibited a substantial drop in response rate over the five months that elapsed between the time he reached criterion and the time he was first placed on the Pr = .80 schedule (Table 4, col 5). Jason, who was a fairly high ranking animal increased his response rates between his criterion trials (col 4) and his being given the Pr = .80 condition for the first time almost 10 months later (col 5). By the time the animals received their first exposure to the .80 reinforcement condition, all tendency for a relationship between former social rank and response rates had completely disappeared.

Table 5 provides a summary of the omission ratio data before, during, and after the formation of the group. Prior to the formation of the group, there was no relationship between omission ratios and the animals' previous social rank in the Yerkes group. After group formation, a relationship between omission ratios and rank appeared such that, across the entire time the group was under observation and testing, there was a positive correlation of $P =$ +.83 (t = 2.98, df 4, p = .04, two-tailed) between high social rank and high R_o. The emergence of this relationship was due primarily to decreases in R_os of the lower ranking animals. Loki, the highest ranking, or alpha, monkey, showed little change in his R_os across the entire study, although he exhibited transient increases after three of the four introductions. Pardner, the third ranked animal, showed the smallest decrease in magnitude of the R_o and it is interesting to note that he was the least active, in terms of participation in agonistic encounters, of all the monkeys in the group.

All of the animals exhibited high, positive correlations between response rates after reinforced and nonreinforced intervals on the FI 1-min schedule prior to group formation. After group formation, this was true for all animals except Tonto, who made too few responses to allow calculation of a correlation coefficient.

In Table 6, the mean response rates after reinforced intervals on the FI 1-min schedule with the P_r = .80 are given for before and after group formation. The response rates for all animals tended to be depressed immediately following their entrance into the social group. The effect was slight in the case of the two top ranked animals, Loki and Kansas. Pardner, ranked third, exhibited an abrupt drop following group formation and his rates continued to decline over the course of the study. The fourth ranked animal, Jason, dropped his rate sharply after being placed in the group and then recovered to produce rates slightly above his preintroduction levels. Tonto, ranked fifth, stopped responding and had not recovered his performance to a point which provided meaningful rate data by the end of the study. Zeus had a high rate of response (12.01) prior to group formation; this dropped quite low (3.03) following his removal from the group, recovered to 8.14 on 10 sessions immediately prior to his reintroduction, dropped slightly following reintroduction and had begun to rise again at the end of testing. The net effect of these changes was a clear difference in response rate between the top ranked three animals and two of the three ranked animals (Tonto was the exception) with the higher ranking animals having the lower response rates.

TABLE 5

Median Omission Ratios (R_o) of Six Male Rhesus Monkeys Before, During and After Social Group Formation

ANIMAL		PRE-INTRODUCTION	GROUP FORMATION 8/26-9/10	JASON IN 9/11-9/23	TONTO IN 9/24-10/7	ZEUS RE-INTRO. 10/8-10/17	X̄ of MEDIANS 8/26-10/17	X̄ of MEDIANS AFTER GROUP FORMATION 8/26-11/20	SOCIAL RANK IN NEW GROUP
LOKI	# tests	21	18	6	9	19	52	101	1
	R_o	2.41	2.80	2.35	2.96	2.59	2.68	2.42	
KANSAS	# tests	21	16	5*	7*	20	48	95	2
	R_o	3.40	2.24	2.43	2.32	2.07	2.27	2.26	
PARDNER	# tests	21	14*	7*	8*	20	49	97	3
	R_o	1.86	2.06	1.89	1.23	1.71	1.72	1.68	
ZEUS	# tests	20	INJURED AND REMOVED - SEE BELOW						-
	R_o	3.06							
JASON	# tests	16		4*	6*	20	30	77	4
	R_o	2.23		1.52	1.79	1.57	1.63	1.61	
TONTO	# tests	29			NO RESPONSE	NO RESPONSE	0*	2	5
	R_o	2.97					0.00	1.33	
ZEUS	# tests	15				13*	13	59	6
	R_o	2.56				1.68	1.68	2.03	

*No response on at least one test under the frustration paradigm (reinforcement p = .80).

Table 6

Mean Response Rates for Six Rhesus Monkeys After Reinforced Intervals on FI 1-min Schedule With Reinforcement Probability of p = .80 Before and After Group Information

RANK	ANIMAL		PRE INTRO-DUCTION	GROUP FORMATION 8/26-9/10	JASON IN 9/11-9/23	TONTO IN 9/24-10/7	ZEUS RE-INTRO. 10/8-10/17	GROUP STABLE 10/18-11/20	MEAN R/R AFTER GROUP FORMATION
1	LOKI	# tests	21	18	6	9	19	49	101
		R/R	3.57	2.96	4.59	3.38	3.81	3.16	3.51
2	KANSAS	# tests	21	16	5	7	20	47	95
		R/R	3.11	2.67	2.22	2.31	2.80	2.45	2.48
3	PARDNER	# tests	21	14	7	8	20	48	97
		R/R	17.95	9.85	7.07	4.49	2.86	1.70	4.61
	ZEUS	# tests	20	INJURED AND REMOVED - SEE BELOW					
		R/R	12.01						
4	JASON	# tests	16		4	6	20	47	77
		R/R	7.24		2.80	10.88	12.96	7.53	8.33
5	TONTO	# tests	29	NO RESPONSE				2	2
		R/R	2.05					1.00	1.00
6	ZEUS	# tests	15				13	46	59
		R/R	6.44				7.22	8.24	7.94

Another effect was the depression of performance seen in all animals immediately following experimental manipulations of the social situation. Even when animals suffered no apparent physical injury during group formation or the introduction of a new animal to the group, performance deteriorated to the point where all of the animals except the alpha, Loki, failed to complete one or more test sessions immediately following the manipulation. In general, the higher the animal's rank and the longer it had been in the group, the less severe was the effect on performance.

Overall, the results of this study supported and extended the findings obtained in the first experiment. Although the relationships between social rank and performance persisted for a while after monkeys were removed from their social groups (first study), they were most apparent when the animals had been but recently removed from their groups or were living in a social group while undergoing social testing (second study). In the formation of the new social group, Loki was the only animal that retained his relative rank with reference to his rank in the old group at the Yerkes field station. Once the initial group of three monkeys was established, the ranks of new-comers subsequently introduced were predictable relationship to their past social histories or previous rank in other groups. Bernstein, Gordon, & Rose (1974) have reported similar findings from studies of group formation in rhesus monkeys, some of which involved the monkeys used in our rhesus experiments. They suggested that a monkey's agonistic rank was of significance only within the context of a given social group.

Thus, our second study provided no evidence that the long term social history of an animal is a major determinant of operant performance. Nor did it suggest the presence of any factor, or constellation of factors, that might predispose an animal to both a particular social role and a particular kind of operant performance. Furthermore, we did not detect any increases in aggressiveness in the social group following test sessions on which omission of reinforcement took place as compared with sessions when the monkeys were receiving reinforcers on 100% of the intervals. There was no evidence that short term experiences in the operant chambers was carrying over to the social situation. We were left with the idea that recent or present social experience resulted in varying degrees of social pressure on the different individuals in the group and that these, in turn, produced predictable effects on operant performance. In particular, the finding that the correlation between rank and omission ratio results from a decrease in R_os in subordinate animals as compared with their R_os when they living alone supports the Strayer (1976) inhibition hypothesis described earlier in this report.

Social Behavior and Omission of Reinforcement in Crab-eating Macaques

(Macaca fascicularis).

At the end of November, 1974, the Yerkes Field Station provided the project with a group of over 50 Macaca fascicularis monkeys to replace the rhesus which we had been using. M. fascicularis, variously known as the crab-eating macaque, the Java monkey, the cynamologous monkey, or the long-tailed monkey,

is a small macaque - adult males weigh only about half as much as rhesus males - that is closely related to M. mulatta. (At one point, some taxonomists had argued that fascicularis was a subspecies of M. Mulatta.) It is a very gregarious species with a well organized social structure. There have been a number of recent studies of the social behavior and organization of this monkey in both the field and the laboratory (e.g., Angst, 1975; deWaal, van Hoof, & Netto, 1976, de Waal, 1977).

The first experiment with these animals sought to confirm our findings from the rhesus studies with the new species. Two troops of animals were formed by dividing the group from Yerkes. The troops, called "T-Troop" and "NT-Troop" adults, subadults, juveniles and infants of both sexes in roughly the same proportions as are found in the wild (Angst, 1975). Matriarchies were kept intact as much as possible when the new troops were formed. The new troops were housed in two compounds identical to those used in the rhesus monkey group formation study described earlier.

The six oldest males in T-Troop were trained on a FI 1-min schedule with Pr = 1.00. There were three adult males, age 6 years and older and three subadult males, ages between 4 and 6 years old at the start of training. In addition, three adult males that had been taken from the original group a year earlier for a pilot study in the laboratory were maintained on the schedule. These animals were isolated from the T-Troop males while the latter were being trained and tested for the first time. The six males from T-Troop were removed from the troop each morning, placed in the operant chambers, and allowed to earn 40 banana pellets on the FI 1-min schedule. They were then placed in individual cages in an adjacent colony room for 30-40 min after which they were given the remainder of their daily food ration (they were maintained at about 95% of their free feeding weights throughout the course of the study). They were then returned to the troop.

Social behavior was observed for one hour per day, weather permitting, while the troop was intact - usually just after the males were returned to the troop following their operant session. The procedures for observing recording and analyzing the social data were quite similar to those used previously with the rhesus monkeys. A behavior inventory was developed for fas cicularis during the late winter and early spring of 1975 (see Table 7). The observers scanned the troop continuously during the observation period and recorded the behavior of the 24 oldest monkeys in the troop as it occurred. Details of the social behavior observations will be found in a separate section of this report.

Performance on the FI 1-min schedule by the six T-Troop males was stable (IC $\geq$ +.40) by early May, 1975, and the animals were shifted to a Pr = .80 for 21 days of testing. They were then returned to a P_r = 1.00 for 32 days. During this time, the reinforcement probability of .80 was introduced as a "probe" on seven occasions, with intervals between probes varying from three to seven days. Then they were placed on a P_r = .80 schedule for nine days, after which Weed, one of the animals from the old pilot group, was placed in T-Troop. Testing on this schedule was continued for two and a half months

Table 7

Java Monkey Behavior Categories

Agonistic Behaviors:

        Aggressive
                Chase
                Threat (open-mouth)
                Charge
                Slaps
                Bites

        Submissive
                Avoid
                Grimace
                Squeal
                Flee

        Other Agonistic *
                Lid
                Lip Smack
                Enlist

Sexual Behaviors:

                Sexual Present
                Mount (no thrusting)
                Mount (with thrusting)
                Masturbate
                Genital Manipulation (other animal)
                Genital Sniff

Other Social Behaviors:

                Present to Groom
                Groom
                Ventral-Ventral Hug
                Ventral-Dorsal Hug
                Sit Next To (physical contact with other
                                animal)
                Play *

Non-Social Behaviors:

                Self Groom
                Move
                Sit - No Social

* "Lid", a flash of the white eyelids, "Lip Smack", and "Enlist" are scored, but are not currently used in the analyses described in the text. Lid is a part of the "pout threat" (Angst, 1975) commonly used by subordinate animals, lip smack is ambiguous and perhaps should not even be classed as agonistic, while enlisting occurs very infrequently in our groups. "Play" occurs only in infant and juvenile animals and is difficult to define reliably.

at which time another adult male, Legs, was introduced into the troop. Two weeks later, a third adult male, Easy, was placed in the group. After two more weeks of testing under a P_r = .80, the animals were returned to a P_r = 1.00. Over the next three weeks, the animals were given two brief periods in which the P_r was set at .90 after which they began training on an entirely new schedule. (See the section on DRL testing for details).

In May, 1976, the 12 oldest males in NT-Troop began training on the FI 1-min schedule with a P_r = 1.00. Perhaps because most of these animals had spent the previous year working on a different operant schedule (a DRL schedule that will be described in the next section of the report), the group did not meet the performance criterion on the FI schedule (IC $\geq$ .40) until September of that year. Eleven of the twelve animals were then shifted to a P_r = .80 for 40 days; there were seven adults and four sub-adults in this group. At this point Ian, the alpha male, was removed from the troop. Eju, the animal that had ranked third became the new alpha male by defeating Knees, the animal that had ranked second when Ian was in the troop. Seven weeks later Ian was returned to the group; he defeated Eju and reestablished himself as the alpha male. Knees regained second place so that the original rankings were re-established.

By the time the T-Troop males were shifted from a reinforcement probability of 1.00 to one of .80 for the first time, agonistic behavior in the troop had dropped to a low level and the male dominance hierarchy appeared to be quite stable. The data obtained during training on the FI schedule and the initial testing with omission of reinforcement were quite different from that which had come out of the studies with rhesus monkeys. In the first place, there was a high, positive (+.83) correlation between basal response rate and social rank. Where low response rates under a P_r = 1.00 had been related to high social rank in rhesus, this was not the case with fascicularis. In fact, the alpha male, Capone, had some of the highest response rates we had ever seen, even when his ICs were well in excess of the +.40 criterion. Second, there was no apparent relationship between omission ratios and social rank when the animals were placed on the P_r = .80 schedule. Shifting the animals back to a P_r = 1.00 and using occasional P_r = .80 conditions as "probes" did not result in the appearance of any relationships between social variables and performance. Throughout testing, the performance of the three adult males was quite different from that of the three subadults being tested. Since the social data indicated that the subadults were minimally involved in the maintenance of the male dominance hierarchy, it was decided to treat adults and subadults as separate groups in analyzing the R_0 data. Overall, the subadults had much higher omission ratios than the adults. Within the subgroup of three adult males, there was no relationship between either response rates or omission ratios and social rank. It was only when we introduced a new male, Weed, into the troop in November, 1975, that we began to see a relationship between social behavior and performance. Weed's introduction produced a marked increase in agonistic behavior in the troop and there was a change in the male hierarchy, with Weed moving into second place in November and becoming the alpha male in December. Intermale aggressive behavior increased sixfold in November over October levels and was still double that of October in December. (See Table 8.)

TABLE 8

Aggressive and Submissive Behavior Matrices for T-Troop Males Before,
During, and After Introduction of Weed*

(A.) OCT '75 (12 Days)

RANK	ANIMAL	CODE	SUBMISSION B	C	A	D	F	E	Total	AGGRESSION B	C	A	D	F	E	Total
1	Capone	B	-	0	0	0	0	0	0	-	0	0	0	3	0	9
2	Madison	C	0	-	0	0	0	0	0	0	-	0	0	1	1	7
3	Gus	A	3	3	-	0	0	0	6	0	0	-	3	1	0	10
4	Oliver	D	2	4	10	-	0	1	17	0	0	0	-	0	6	16
6	Cracker	F	5	4	6	0	-	1	17	0	0	0	1	-	1	5
8	Spiro	E	3	2	1	9	2	-	20	0	0	0	0	0	-	1

(B.) NOV '75 (12 Days) Weed Introduced

RANK	ANIMAL	CODE	SUBMISSION B	U	C	A	F	D	E	Total	AGGRESSION B	U	C	A	F	D	E	Total
1	Capone	B	-	2	0	0	0	0	0	2	-	14	1	4	1	4	0	50
2	Weed	U	27	-	11	0	0	0	0	39	0	-	5	0	2	3	2	20
3	Madison	C	4	12	-	2	0	0	1	19	0	12	-	1	1	4	4	23
4	Gus	A	5	9	5	-	0	0	0	19	0	1	2	-	4	8	8	33
6	Cracker	F	8	10	5	13	-	0	0	37	0	1	0	0	-	1	4	13
9	Oliver	D	5	8	7	18	0	-	0	40	1	21	0	0	1	-	4	38
10	Spiro	E	1	3	6	14	2	5	-	35	0	0	2	0	0	0	-	7

(C.) DEC '75 - JAN '76 (11 Days)

RANK	ANIMAL	CODE	SUBMISSION U	B	C	A	D	F	E	Total	AGGRESSION U	B	C	A	D	F	E	Total
1	Weed	U	-	0	0	0	0	0	0	0	-	0	1	1	0	0	0	4
2	Capone	B	5	-	0	0	0	0	0	6	0	-	0	4	0	3	0	11
3	Madison	C	10	0	-	0	0	0	0	10	0	0	-	4	0	0	0	12
4	Gus	A	10	15	7	-	0	0	0	33	0	0	1	-	0	3	5	31
5	Oliver	D	2	1	1	1	-	0	0	5	0	0	0	0	-	3	2	10
6	Cracker	F	2	0	1	8	6	-	0	18	0	0	0	0	0	-	2	4
7	Spiro	E	0	7	2	7	7	2	-	25	0	0	0	0	0	0	-	3

* Ranks are determined on the basis of defeats. Data are given only for males being tested on laboratory tasks. Where ranks of males are not consecutive, adult females hold the intervening positions. Reading the matrix horizontally indicates the number of times the animal "does" the behavior to each other animal. Reading vertically give the number of times the animal "receives" the behavior from the other animals. For example, in the November matrix, Capone ("B") submits twice to Weed ("U") and aggresses against him 14 times; Weed submits to him 27 times and Capone receives only one aggressive response, by Oliver ("D") during this period. The total number of response directed toward all animals in the troop by each male is given at the right of each matrix in the "total" column. Further details may be found in the text.

The operant data covering the period before, during, and after the introductions of Weed, Legs, and Easy into T-Troop are summarized in Table 9. Weed's introduction was accompanied by an increase in the omission ratios of both Weed and Capone, the alpha male. Madison, who lost second rank to Weed, exhibited a substantial drop in his R_0, while Gus's R_0 was unchanged. The R_0's of all four animals were elevated in December, and there was a close relationship between rank and magnitude of the omission ratios during that month. This disappeared in January, prior to the introduction of Legs. With Legs' introduction, the three top ranked monkeys again showed increases in their R_0s. However, this was also the case for Legs, despite the fact that he was defeated by all four adult males. Easy's introduction was accompanied by another increase in Weed's R_0. Easy defeated Capone and Madison and assumed second position in the male social hierarchy. The omission ratios of Capone and Madison dropped after Easy entered the group. The same was true to a lesser extent for Legs, who dropped to ninth in rank in the male hierarchy during this time. Gus was not as involved in the agonistic interactions following Easy's introduction as were the other adults - he submitted immediately and avoided extensive confrontations with the very aggressive Easy. Gus's R_0 increased during the two weeks following Easy's introduction. The expected rise in Easy's R_0 did not occur, however; instead, his ratios fell from fairly high levels -- greater than 2.0 -- to very low levels -- less than 1.0 -- following his introduction into the troop. This change was accompanied by a substantial drop in responses per reinforcement on reinforced intervals. All omission ratios were relatively low and unrelated to rank during the last two weeks of February when agonistic interactions had fallen to a low level in the troop.

As noted earlier, the three subadult males tended to have the highest R_0s throughout the study. Considering them as a subgroup, the magnitude of their R_0s reflected their relative ranks prior to and during the first month after Weed was introduced and again at the end of the study. However, the relationship was not present during December, January, or the first two weeks of February.

An examination of the correlations between each animals daily response per reinforcement (R/R) and its omission ratios showed that Legs and Easy were handling the contingencies of the operant schedule in a different manner than all seven of the other males being tested in T-Troop. These correlations for 20 weeks, from October 1975 through February 1977, are listed below, together with the animals' relative ranks at the end of the experiment:

Relative Rank	Animal	r between R_0 and R/R
1	Weed	-.31
2	Easy	+.96
3	Capone	-.38
4	Madison	-.46
5	Gus	-.48
6	Oliver	-.55
7	Cracker	-.66
8	Spiro	-.78
9	Legs	+.88

Table 9

Social Rank, Median Frustration Ratios (R_o) and Responses/Reinforcement (R/R) for Male <u>Fascicularis</u> (T-Troop)*

	Original Group October			November			Weed Introduced December			January			Legs Intro. January			Easy Intro. Jan-Feb			Last 2 Weeks February		
Animal	Rank	R_o	R/R	Rank	R_o	R/R	Rank	R_o	R/R	Rank	R_o	R/R	Rank	R_o	R/R	Rank	R_o	R/R	Rank	R_o	R/R
Capone	1	1.70	79	1	1.97	61	2	2.19	33	2	1.97	27	2	2.08	18	3	1.51	47	3	1.40	42
Madison	2	2.30	4	3	1.70	3	3	2.22	2	3	1.96	6	3	2.49	4	4	1.85	9	4	1.35	10
Gus	3	1.57	13	4	1.56	8	4	1.76	8	4	1.73	9	4	1.50	10	5	1.87	8	5	1.55	9
Weed	-	1.68	6	2	2.04	5	1	2.77	5	1	1.73	18	1	2.00	16	1	2.23	18	1	1.80	14
Legs	-	---	-	-	---	-	-	1.43	8	-	1.95	11	5	2.16	11	9	1.95	11	9	1.85	9
Easy	-	---	-	-	---	-	-	---	-	-	2.18	17	-	2.06	20	2	0.65	3	2	0.99	7
Subadults:																					
Oliver	4	3.69	12	5	3.78	11	5	4.18	4	5	2.52	7	6	2.22	14	6	1.97	12	6	2.30	13
Cracker	5	2.99	8	6	3.52	4	6	-Ill-		6	2.66	7	7	2.47	9	7	2.02	8	7	2.10	7
Spiro	6	2.40	8	7	2.86	4	7	4.42	2	7	3.32	3	8	3.15	4	8	2.57	5	8	2.08	5

* Social rank is relative rank between males, not rank in entire group. (Oliver, Cracker, Spiro and Legs are often outranked by one or more adult females).

In Legs and Easy, omission ratios were low on days when response rates were low and high on days response rates were high. In the other seven animals, where there were trends toward relationships between social rank and omission ratios, high R_os were associated with low responses per reinforcement and vice versa. There was also an interesting, but very complex, relationship between rank and performance in that rank was inversely related to the magnitude of the negative correlations between omission ratios and responses per reinforcement in seven animals. This indicates that if animals exhibit a negative relationship between R_o and R/R in their handling of the schedule contingencies, then the stronger the relationship, the lower the social rank of the animal. In other words, omission ratios are relatively independent of response rates in high ranking animals, but this is true only in animals which habitually show a response pattern in which high R_os are associated with low baseline response rates and vice versa.

One other change of interest took place in T-Troop. During and immediately after the time they were defeated by Weed, the FI performance of Madison and Gus deteriorated. ICs following reinforced intervals dropped from criterion levels to near zero, indicating that the FI scallop had completely disappeared. Capone's ICs dipped slightly following his loss to Weed in late December and sharply, from +.39 to +.18 during the week after Easy's introduction to the Troop and Capone's defeat by Easy. Smaller decreases in ICs were seen in Weed and Easy after their introductions; no changes in ICs were seen in Legs or any of the three subadult males.

The correlation between responses/reinforcement and social rank prior to the introduction of the P_r = .80 condition was +.68 in the seven adult males in NT-Troop. With only five degrees of freedom, this correlation was not significant (p = .09, two tailed) but when we correlated responses/reinforcement with frequency of submissive behaviors in these animals, the rho of -.82 gave a p = .02. The relationship disappeared, however, when all 12 of the males were included in the analysis. (This may have been due to an age group difference, or it may simply have reflected the different past experience with the operant testing situation of the subadults.)

After the NT-Troop males were shifted to a reinforcement probability of .80, there was no apparent relationship between the magnitude of the R_os and any of the social measures, including rank. Ian's removal and replacement produced very little agonistic behavior in the troop, although Eju did become dominant over Knees during Ian's absence. Similarly, when Ian returned, he reassumed the role of alpha male with very little aggression and Knees, allied with Ian, slipped back into second rank. During all this time, there was no relationship between rank and omission ratios. This was true, even when the data from the subadults were excluded from the analysis. Indices of curvature were generally high, and remained unchanged throughout. Knees' R_o dropped rather sharply following Ian's removal, from 2.43 to 1.67 and Eju's R_o from 6.38 to 2.61 following Ian's return. In each case, the decrease was temporary, and lasted about two weeks.

The omission ratios exhibited by three adults in NT-Troop, Knees, Eju, and Barker, were generally much higher than those of any of the adult males of T-Troop. This may have reflected a transfer of DRL response patterns to the FI schedule in these animals. Analysis of the correlations between R_Os and R/Rs yielded a pattern similar to that seen in T-Troop. Ian and Daque had low positive correlations, the other five adults showed negative correlations:

Relative Rank on 11/29		r between R_O and R/R	Relative Rank on 1/7		r between R_O and R/R
1	Ian	+.15	(out of group) Ian		(-.32)
2	Knees	-.47	1	Eju	-.06
3	Eju	-.63	2	Knees	-.64
4	Alabama	-.44	3	Alabama	-.74
5	Barker	-.48	4	Barker	-.75
6	Quotation	-.78	5	Quotation	-.83
7	Daque	+.25	6	Daque	+.36

Overall, the results of the study were disappointing. Most of the *fascicularis* seemed to deal with the contingencies of the FI schedule in a manner that was quite different from that used by the majority of the rhesus monkeys in the earlier studies. Although there was some evidence that changes in performance were associated with changes in the social hierarchy of the Troops, particularly in T-Troop where there was considerable agonistic activity following the introduction of new males, the nature of the changes was not completely consistent with the interpretations we had given the rhesus data. This led us to modify our approach to the omission paradigm. These changes will be described next.

Social Behavior and "Frustration" in M. fascicularis.

In this study we set out to develop a procedure which would overcome some of the difficulties we felt were inherent in the FI schedule we had been using. Following omission of reinforcement, the response bursting which produces R_Os greater than 1.00, might be due to the frustrative effects of nonreward (Amsel, 1958) or to a failure of response inhibition normally correlated with delivery of the reward -- i.e., the higher rate of response following omission of reward occurs because the animals fail to pause and eat a food pellet (Staddon, 1972). The two possibilities are confounded in an FI schedule because the schedule permits a temporal discrimination to be made concerning the time of pellet delivery. Response rates increase toward the end of the fixed interval and produce the typical FI "scallop" response curve. To overcome this problem, we went to a random interval schedule where the probability of the next reward did not depend on the amount of time elapsed since the previous reward was delivered. We also developed a manipulandum which we felt had considerable face validity with regard to the concept of frustration. The manipulandum consisted of a food hopper with a clear plexiglass door. A press on the door constituted a response on the part of the animal, and the door was automatically unlatched when the schedule contingencies

were met. The hopper was illuminated and the animal could see a banana pellet behind the door at all times while he was responding. On reinforced trials, the monkey could obtain the pellet by pressing on the door after the door was unlatched by the program. On nonreinforced (frustration) trials, a solenoid opened the bottom of the hopper so that the pellet disappeared just as the animal reached for it so that the door opened on an empty hopper. Responses (door presses) following nonreward were used to compute omission ratios in the usual way.

The PDP-8 laboratory computer was used to program and run a Random Interval 1-min schedule. The same 21 males from T- and NT-Troops that had participated in the FI experiments were trained until their performance stabilized on the new schedule with a $P_r = 1.00$. The animals were then shifted to a $P_r = .90$ with reinforcement being randomly omitted on 10% of the completed intervals. Local response rates were recorded for interpellet intervals following both delivery and omission of pellets. Daily one hour social observations were taken during the duration of the experiment.

After the animals had been on a $P_r = .90$ for two weeks, the alpha male was removed from each of the two troops. After three weeks, the new alpha males were removed and the original alphas returned to their respective troops. Three weeks later, an intermediate ranked animal was removed from each troop and the animals that were out of the troops returned. After three more weeks, the two intermediate ranked animals were returned and testing continued with the troops intact.

There were two results of interest. First, 15 of the 20 males which exhibited stable performance on the random interval schedule had higher response rates at the beginning of the nonreinforced component of the schedule than at the beginning of the reinforced component (i.e., their R_Os were consistently greater than 1.00). This was true during the first 12 seconds of the intervals. In general, response rates following nondelivery of reward were greater than rates following delivery of reward for the first 36 seconds of the intervals and then diminished during the later portions of the intervals. In terms of overall response rates, 8 of 9 T-Troop males and 7 of 11 NT-Troop males made more responses in the nonreinforced component than they did in the reinforced component. These data indicate that it is possible to obtain response bursting -- "frustration effects" -- on a schedule that does not involve the fixed interval schedule's temporal response patterning.

Second, there was a relationship between social rank and performance in T-Troop, but not in NT-Troop. This was consistent across our attempts to manipulate the social organization of the troops by removing and replacing animals in the two troops. The data for the baseline period, prior to the first social manipulation, yielded a rho of +.70 between rank and local rate omission ratio (df = 7, p = .04) in T-Troop. (Local Rate Omission Ratio, or LR_O, is the omission ratio calculated for the first 12 seconds of the intervals following nonreinforcement and reinforcement.) There was no such relationship between rank and performance in NT-Troop.

The data for the periods covering the removal and replacement of the alpha males in both troops are presented in Table 10. In T-Troop, removal and replacement of the alpha male the first time produced a considerable increase in agonistic activity in the troop and correlations between rank and performance

Table 10

Performance by Males from Two Troops of <u>Fascicularis</u>
Monkeys on a Random Interval 1-Min Schedule where P_r = .90

Rank	Monkey	Mean Response Rate			Initial Local Response Rate		
		Reinf.	Nonreinf.	Ratio	Reinf.	Nonreinf.	Ratio
T-Troop:							
1	Easy	4.61	6.07	2.34	3.13	5.42	1.73
2	Capone	18.29	30.23	1.65	17.45	32.86	1.83
3	Madison	16.46	17.45	1.06	10.90	21.18	1.94
4	Weed	45.80	49.96	1.09	28.57	40.50	1.42
5	Gus	11.89	14.25	1.20	13.09	16.94	1.29
6	Cracker	9.65	10.39	1.08	20.00	20.00	1.00
7	Spiro	28.06	35.33	1.26	31.80	40.38	1.27
8	Oliver	99.05	107.05	1.08	81.62	87.50	1.07
9	Legs	18.65	15.76	.84	30.82	22.00	.71
	Rho with Social Rank:	.45		-.66			-.90
NT-Troop:							
1	Ian	34.04	28.17	.83	26.95	30.00	1.11
2	Knees	2.75	3.70	1.34	4.74	2.86	.60
3	Alabama	17.82	23.34	1.31	16.50	20.00	1.21
4	Eju	1.75	2.83	1.61	.10	.19	1.90
5	Barker	65.66	63.21	.97	40.75	54.17	1.33
6	Tag	14.55	24.22	1.66	25.05	52.73	2.10
7	Quotation	8.54	9.87	1.16	12.40	17.50	1.41
8	Equal	10.95	3.47	.32	11.57	12.50	1.08
9	Yuk	73.82	73.92	1.00	66.87	73.40	1.10
10	Hobbit	28.31	36.68	1.30	33.07	42.14	1.27
11	Daque	3.62	4.19	1.16	11.57	10.77	.93
	Rho with Social Rank	.10		-.15			-.01

Adapted from Adams, Allen, & Bunnell, 1977.

increased to +.66 between high rank and high R_0 and to +.90 between high rank and high LR_0. By the end of the study and the completion of all social manipulations, the correlation between rank and LR_0 was still a significant +.68. In between social manipulations, the correlations between R_0s and rank tended to drop off to +.40 to +.50, but would rise again to about +.70 when the manipulations were being made. As can be seen from the table, no such relationships were apparent for NT-Troop. In NT-Troop, in contrast to T-Troop, there was little agonistic activity between the adult males and the social manipulations did not produce either a marked increase in aggression or any profound alteration of the social rank structure. Perhaps, at least in M. fascicularis, social behavior/performance relationships are manifest only when active tensions exist within a group and the social structure is under pressure. On the other hand, it might just be that the combination of animals in T-Troop was somehow unique and this resulted in the appearance of significant correlations.

To examine this matter further, the study was repeated with a new troop of animals. This group, named I-Troop, consisted of nine males, drawn from both T- and NT-Troops and formed into an all male troop during the spring and summer of 1978. Because an imbalance had developed in the age/sex categories of the two breeding troops -- there were too many adult and subadult males relative to the number of adult females in both troops -- we removed three adult and two subadult males from T-Troop and four adult males from NT-Troop in April, 1978. The animals were isolated from each other until the middle of May at which time we began to put them together to form I-Troop. Seven males were introduced into a compound simultaneously. The social behavior of this group was observed for two weeks whereupon the eighth male was introduced. Two weeks later, the ninth animal was placed in the group. During the periods of isolation and group formation, testing was continued on the random interval schedule with a P_r = .90. A summary of the omission ratio data during this time is given in Table 11. (LR_0s were similar, but more variable). The overall correlation between the mean omission ratio during group formation was +.74 (p = .02, two tailed) between high R_0 and high rank. With the two subadults excluded, it was +.83. Also, during the two weeks following Alabama's introduction -- he bacame the alpha male during this time -- the correlation between rank and LR_0 rose to +.94.

During the last year of the project, this study was repeated with I-Troop. Eight animals (Daque had died) were retrained on the Random Interval 1-min schedule with a P_r = 1.00 for seven weeks. They were shifted to a P_r = .90 for 10 weeks during which time Alabama, the second ranked animal at that time, was removed and replaced and two new animals, Grandpa and Quotation were placed in the troop.

The animals were shifted from P_r = 1.00 to P_r = .90 on the first of August, 1980. The rank order correlation between social rank and R_0 for that day was +.85. Unfortunately, Alabama's performance had deteriorated prior to this time and he was not completing his daily test sessions. He was not shifted to the omission of reinforcement and so his data could not be included in the analysis. He was removed from the troop and retrained. (Although he began completing sessions after several more weeks, he never was shifted to the P_r = .90 condition.) Alabama's removal produced no change in the social hierarchy.

Table 11

I-Troop Omission Ratios,
VI 1-Min Schedule, May-June 1978

Animal	Animals Isolated May 1-15		Group Formed May 16-22		Alabama In May 31-June 12		Cracker In June 14-23		X̄ OR while in group
	Rank	OR	Rank	OR	Rank	OR	Rank	OR	
ALABAMA	-	1.18	-	(1.35)	1	1.49	1	1.17	1.33
GUS	-	.95	T-1	1.06	2	1.36	2	1.11	1.18
SPIRO	-	1.41	T-1	1.05	3	1.08	3	1.23	1.12
EQUAL	-	1.05	6	1.32	4	1.33	4	.89	1.18
CRACKER	-	1.02	-	(.99)	-	(.66)	5	1.02	1.02
DAQUE	-	.91	7	1.05	5	.62	6	1.19	.95
*NOD	-	1.00	T-4	1.03	T-6	.83	T-7	.99	.95
*YAMAMOTO	-	.99	T-4	1.06	T-6	1.09	T-7	.94	1.03
YUK	-	.69	3	1.13	8	.97	9	1.07	1.06

* Subadults and allies

The mean of the median R_0s for the three highest ranking animals was 1.36 and for the four lowest ranking animals it was 0.76 for the first two weeks of August (7 test sessions). Due to computer software problems, the remaining data from this study had to be analyzed by hand and the results of these analyses were not available at the time this report was being prepared. Nevertheless, the results that are available from this replication confirm and support the earlier findings.

Overall, the data from the omission of reinforcement studies done with fascicularis differed from that obtained from the rhesus monkeys in that baseline responding on a fixed interval schedule tended to be low in high ranking rhesus and low in high ranking fascicularis. There was evidence that the two species tended to handle the contingencies of the FI schedule differently. When omission of reinforcement was introduced, the omission ratios of the rhesus were relatively independent of baseline FI responding. This was not the case in fascicularis in which a majority of the animals exhibited high positive correlations between R_0s and responses per reinforcement. When a random interval schedule was given to the fascicularis monkeys, a relationship between high social rank and high R_0s appeared which was similar to that found in rhesus with the FI schedule. In both species, the relationship was strongest when the animals were engaging in considerable agonistic activity in their groups and/or when shifts in social rank were taking place.

Social Behavior and DRL Performance in M. fascicularis.

Our interpretation of the results of the studies with rhesus monkeys suggested that high R_0s, i.e., more response bursting, by high ranking animals might be related to greater tendencies toward response inhibition by low ranking animals. At the time we began testing the male fascicularis from T-Troop on the FI 1-min schedule with omission of reinforcement in 1975, we also began testing the males in NT-Troop on a DRL schedule, a schedule which requires that an animal withhold its responses for a given period of time if it is to be rewarded.

On a DRL schedule (differential reinforcement of low rate) with a limited hold (LH) contingency added to it, the animal must refrain from responding until a predetermined time has elapsed and then must make the appropriate response before another arbitrary time period has elapsed. In the DRL 18-sec LH 5-sec schedule we used, a lever press made within a 5-sec window beginning 18 sec after a reinforcement was received results in another reinforcement. Shorter or longer interresponse times (IRTs) are not reinforced and simply reset the 18 sec delay requirement.

Typical performance on a DRL schedule results in a modal interresponse time which just exceeds the criterion value -- in this case, 18 sec. However, a significant portion of the total responses in a session consists of a series of very short IRTs (response bursts) which often occur following the making of a nonreinforced response. It has been argued that these response bursts are a manifestation of frustration produced by an unreinforced response which, of course, extends the temporal requirement for the next available reinforcement. High "frustration" would be shown by a high response to reinforcement ratio.

In addition, a relatively independent measure of timing efficiency is provided by calculating the median and variance of the IRT distribution from which the response bursts in the first bin have been deleted. An efficiency ratio, the ratio of the total number of responses to the number of reinforced responses, is also a useful measure.

Testing of the NT-Troop males was begun in the spring of 1975 with the six oldest males in the troop, five adults and one subadult. Later in the year, three more subadults from the troop were trained as well as a new adult male that had not been in the group before. (He was introduced into NT-Troop in the winter of 1976.) In the fall of 1975, three attempts were made to manipulate the social environment of the animals by removing and then replacing key males in the social hierarchy. Training and testing of the nine oldest males in T-Troop was initiated in the spring of 1976 and lasted for about a year. Testing included several removals and replacements of certain males.

Perhaps because of their previous experience on the FI 1-min schedule, the males in T-Troop did not reach the level of performance during training that the NT-Troop males achieved. Most NT-Troop males had efficiency ratios below 2.00 -- less than two responses per reinforcement received -- and few T-Troop animals were this efficient. This meant that it was not possible to combine the absolute scores from the two troops in any meaningful fashion. However, within each troop, there were two consistent relationships between social variables and performance. The relationships were present in the 8 adults and 1 subadult tested in T-Troop and for the 5 adults, but not the 4 subadults from NT-Troop a year earlier. In Table 12, the raw data are shown during acquisition training on the DRL and following a removal and replacement of the alpha male, Knees. In Table 13, the correlation coefficients between rank and efficiency ratios and between frequency of aggressive responses and response bursting are given for the nine males in T-Troop before and after the removal and replacement of Weed, the alpha male.

In both troops, high ranking males reached and maintained higher levels of efficiency (low efficiency ratios) on their DRL performances sooner than lower ranking animals. In both troops, high frequency of aggressive responses was correlated with a high level of response bursting during periods when experimental social manipulations were conducted.

During the last few months of the project, from April through September, 1980, the animals were placed back on the DRL schedule to see if the relationships continued to hold. There was relatively little agonistic behavior in the two troops during those months, although there was more aggression in NT-Troop than in T-Troop, and no social manipulations were made because of an experimental study of affiliative behavior was being conducted at the same time. (Details of the affiliative behavior study may be found in the section on social behavior later in this report.)

At this time there were eight adult males in NT-Troop. The mean efficiency ratios during retraining, after the animals were shifted to a limited hold contingency, was 2.03 for the three top ranked males and 6.26 for the other five -- there was no overlap between the high and low rank groups. The rank order correlation between high rank and low efficiency ratio was a statistically significant +.71. With only five males under study in T-Troop, the rank order correlation of +.81 between low efficiency ratio and high rank may not reflect a real relationship. However, the alpha male had the lowest efficiency ratio and the lowest ranking male the highest, 1.71 and 3.43, respectively.

Table 12

Performance on DRL 18-Sec LH 5-Sec Schedule by NT-Troop Males

A. Social Rank and Trials to Reach Efficiency Ratio<2.00
B. Social Rank, Response Bursting (1st Bin IRT/OPS) and
   Frequency of Aggressive Responses Following Knees'
   Reintroduction.

A. _Acquisition:_

B. _Social Group Manipulation_

ANIMAL	TRIALS TO R/R<2.00	RANK	TOTAL AGGRESSIVE RESPONSES	RESPONSE BURSTING (IRT/OPS - 1st BIN) KNEES' 2nd INTRO.	RANK
Knees	49	1	13	.31	3
Barker	69	2	41	.41	2
Eju	Never Consist. 2.00	4	8	NA*	6
Alabama	84	5	12	.29	1
IAN	94	6	4	.14	5
Quotation**	53	22	1	.23	22

* Performance deteriorated - had to be retrained
** Subadult Male

Table 13

DRL Performance and Social Variables

Group T

	Group Intact to 11/18/76	Weed Removed 11/19/76-12/15/76	Group Intact from 12/16/76
Efficiency/ Social Rank	rho = +.77	rho = +.80	rho = +.88
Aggression/ Bursting	= +.77	N.S.	= +.68
Relative Ranks:	Weed Easy Capone Madison Gus Oliver Cracker Spiro Legs	Easy Gus Capone Madison Oliver Cracker Spiro Legs	Easy Gus Capone Weed Madison Oliver Cracker Spiro Legs

In summary, high ranking males tended to be more efficient in their DRL performance than lower ranking animals. In these monkeys, response bursting tended to be associated with a high frequency of aggressive responses in the social group, regardless of rank in the dominance hierarchy.

Social Behavior and Changeover Ratio Performance in M. fascicularis.

Following removal of the ine males in I-Troop from T- and NT-Troops, a new study was undertaken with the remaining males. The one operant task we had looked at in which we found high ranking animals consistently outperformed low ranking animals was the DRL schedule. (See the preceding section.) On this schedule, the higher ranking animals achieved better (lower) efficiency ratios more quickly than lower ranking animals during acquisition. To pursue this finding further, six T-Troop and eight NT-Troop adult males were trained on a changeover ratio schedule. The rationale for this study involved the idea that certain abilities might predispose an animal toward high rank and that the ability to "count" accurately would be a meaningful component of efficient behavior. Such an ability might be particularly relevant to social monkeys whose well-being depends upon their ability to discriminate and keep track of their positions within the group with respect to each other member. The changeover ratio schedule provides a measure of counting accuracy.

The monkeys were trained to press a lever 12 times after which a changeover to a second response, in this case a press of the door on the hopper manipulandum, produced a banana pellet. Responses on the changeover manipulandum which followed too few responses on the lever were not reinforced, but instead reset the 12 response requirement on the lever. As usual, the animals were allowed to earn 40 banana pellets during each daily session.

Data were recorded in sixty response bins according to the number of lever presses the animal made before pressing the door of the hopper. (The sixtieth bin was an overflow counter.) From this, the median number of number of lever presses made prior to a changeover was calculated as were the interquartile range and total number of response sequences initiated by the animal. (A sequence was scored each time an animal made one or more lever presses prior to pressing the hopper door.) One bin, the "0" bin, recorded successive presses on the hopper door without intervening lever presses. This measure was felt to be akin to the response bursting seen with omission of reinforcement under the random interval schedule described earlier.

Training of the 14 males was begun in January, 1978. In April, Weed was removed from T-Troop and Knees was taken out of NT-Troop. These animals continued their training along with the others, but were kept in social isolation for several months. Training on the schedule took a long time, particularly for the males in NT-Troop. At the end of June, Knees was introduced into T-Troop and, a few weeks later, Weed was placed in NT-Troop.

As the animals began to reach stable levels of performance early in the summer, the higher ranking animals were approaching a modal response frequency of 12 presses per sequence more quickly than the lower ranked animals. This is demonstrated in Table 14 which shows the data prior to the introductions of Knees and Weed. Easy, the alpha animal in T-Troop, was performing very well. His median presses per response sequence of 12.26 was very close to the schedule requirement of 12, there was little variation around this median (2.84), and he wasted little effort on repeated presses of the hopper door. The overall trends between rank and performance are quite apparent from the table. Even though Oliver, Legs, and Tag wasted a lot of effort, they usually managed to collect their 40 food pellets in a session. Quotation was interesting; he could "count," but only up to eight. When the schedule requirement was raided to nine, he pressed the lever eight times, pressed the door, and, when it wouldn't open went and sat in a corner for the rest of the test session.

Once most of the animals had stabilized their performance at or near 12 responses per sequence, however, relationships between social behavior and performance disappeared. Neither the introduction of Knees and Weed nor the removal and replacement of the alpha males during September produced any correlations of significance in either troop. A shift to a reinforcement probability of $P_r = .80$ was introduced but, while it resulted in some bursting, it did not produce reliable relationships between performance and either rank or agonistic behavior frequency. This reinforcement omission paradigm was carried through three removals and replacements of males of varying status in the group without notable success. The study was terminated in the spring of 1979.

TABLE 14

Performance on Changeover Ratio of 12 : 1
June 14-23, 1978

T-TROOP:

Animal	Rank	Median Presses/ Sequence	Inter- quartile Range	"O" Bin Responses (Proportion)
EASY	1	12.26	2.84	.15
CAPONE	2	10.06	6.49	.34
MADISON	3	9.51	7.58	.39
OLIVER	4	.86	7.14	.59
LEGS	5	.77	5.77	.60

NT-TROOP:

Animal	Rank	Median Presses/ Sequence	Inter- quartile Range	"O" Bin Responses (Proportion)
IAN	1	13.68	5.37	.23
EJU	2	13.74	2.46	.10
BARKER	3	18.70	3.62	.06
TAG	4	.89	.65	.56
ARISTOTLE	5	10.52	7,59	.44
*QUOTATION	6	.91	4.00	.56
**HOBBIT	7	9.17	6.53	.38

*Working under a ratio of 8:1

**Subadult

Social Behavior and Complex Problem Solving in M. fascicularis.

In the two studies completed with rhesus monkeys which were described at
the beginning of this report, the high ranking animals made fewer responses
per reinforcement on the fixed interval operant schedule than did the low
ranking animals. In other words, they were more efficient than the low
ranking animals in dealing with the schedule contingencies. It might be
argued, then, that a monkey's social status is, at least in part, determined
by his efficiency in his relationships to his environment, especially to the
complex social processes in which he is involved. We hypothesized that, if
such were the case, then high ranking animals ought to perform better on
complex problem solving tasks than low ranking tasks. Three experiments
were conducted with M. fascicularis to test this idea:

Social Rank and Object Concept Formation. The first study (Czerny and
Bunnell, 1977) was done as a Master's thesis project by Mr. Paul Czerny and
was designed primarily as a test of the monkeys' ability to learn tasks
indicative of the stage VI level of development in Piaget's (1970) theory
of cognitive development. Since social data were also being collected on the
subjects - the three adult and two oldest subadult males in T-Troop prior to
the introduction of Weed, Easy and Legs - it was possible to look for relation-
ships between task performance and social variables.

Testing was done in a modified Wisconsin General Test Apparatus (WGTA)
and involved training and testing on tasks designed to demonstrate whether
the animals could learn the concepts of "object permanence" and "sameness-
difference." The results indicated that the animals could solve a conceptual
task using an object concept indicative of Piaget's stage IV level of cognitive
development. Prior claims for stage VI development in nonhuman primates were
not upheld because the animals used object position as a defining characteristic
of the stimulus objects. Comparisons of performance across the six phases
of training and testing conducted with these subjects did not reveal any clear
relationships between learning and social variables. The alpha male of the
troop, Capone, tended to do worse than the other four animals - he was relatively
inflexible in the response strategies he adopted - but their performance was
not reliably correlated with their rank.

Social Behavior and Visual Discrimination Reversal Learning. At the same
time that the study described above was being run with the T-Troop males,
we began training and testing of the adult males in NT-Troop on a black-white
visual discrimination reversal task. Later, the T-Troop males were also
tested on this task. A total of 17 males from the two troops completed
testing over a period of about two years (Bunnell, Gore, and Perkins, 1980).

The WGTA used in the experiment consisted of a stainless steel cage
60x60x70 cm high, a moveable tray, painted gray, that could be slid forward
to present the stimuli to the animals, and a wooden screen that was lowered
between the cage and the tray between trials. When the screen was raised,
the animals could reach the stimulus tray through an opening in the cage.
A plexiglass window, mounted just above this opening, enabled the subjects
to see the tray. The stimulus tray contained two food wells, 4 cm in diameter,

1.25 cm deep, 15 cm apart and 6 cm in from the front edge of the tray. A 60
watt frosted incandescent light bulb, mounted directly over the stimulus tray
was the only illumination in the test room which was flooded with 65 db
white noise to minimize external noises. The discriminanda were two wooden
cubes (6 cm^3), one painted black and the other white. Raisins were used to
reinforce correct responses. The intertrial intervals were 30 sec and the
problem was presented to the monkey for 10 sec or until the animal made a
response. Each daily session lasted for 40 trials or until the animal failed
to respond on 10 consecutive trials.

Following adaptation to the test situation and pretraining on the required
responses, the animals were trained to a criterion of 36 correct responses out
of 40 trials for two consecutive days. Either the black or the white cube
was always correct on this initial learning of the discrimination, with the
location of the cubes being changed from trial to trial according to a Gellerman
series. On the session after criterion was reached on initial learning, the
first reversal was presented. That is, the formerly positive stimulus became
the negative stimulus and the negative stimulus became positive. When the
monkey reached criterion on this task, the stimuli were reversed again. All
nine of the T-Troop males and five of the eight NT-Troop males completed at
least 10 reversals.

Weather permitting, the social behavior in each troop was recorded for 1
hour each day, five days a week. All of the animals in this study were also
undergoing operant testing during the period of this study. Eight of the nine
males from T-Troop used in the study had previous experience in the WGTA as
either pilot animals or subjects in the object concept study described earlier.
The NT-Troop males had no prior WGTA experience. During the period WGTA testing
was in progress, NT-Troop remained intact. Three social manipulations,
involving removing and replacing males, were conducted during the time T-Troop
males were undergoing reversal testing.

In analyzing the data, the performances of the three highest ranking males
in each troop were considered together and compared with the performances of
the remainder of the males tested from the two troops. (The low rank group
consisted of 11 animals for the analysis of initial learning and of the first
reversal and of 8 animals for analysis of the 2nd-10th reversals).

As can be seen from Table   15   and Figure   1   , high ranking animals
made more errors than low ranking animals on both initial learning and re-
versal learning. The response patterns exhibited by each animal were examined
using a modification of a procedure suggested by Levine (1965) for the study
of hypothesis behavior. Each day's test on each animal was divided into con-
secutive sets of three trials each, beginning with the first trial of the day
(and ignoring trial 40). Sets with no errors were classified as correct;
those with one or more errors were classified according to the pattern of
errors present into the following categories: position preference, object
preference, or response shift. The last category was further subdivided into
lose-shift, win-shift and random-shift strategies. There was no relationship
between the types of error patterns characteristic of an animal and either his
trials to criterion or his social rank. Additional details of the results of
this experiment can be found in the published report (Bunnell, et al., 1980a).

Table 15

Mean Errors to Criterion During Acquisition and Reversals of a Black-
White Discrimination Problem by High and Low Ranking Male Fascicularis
(High rank N=6. Low rank N=11 on acquisition and first reversal and N
= 8 on reversals 2 through 10.)

| Group | Acquisition | Reversals | | |
		1	2-4	5-7	8-10
High Rank	64.67	134.17	105.00	46.83	36.67
Low Rank	37.09	88.45	45.37	18.88	11.38
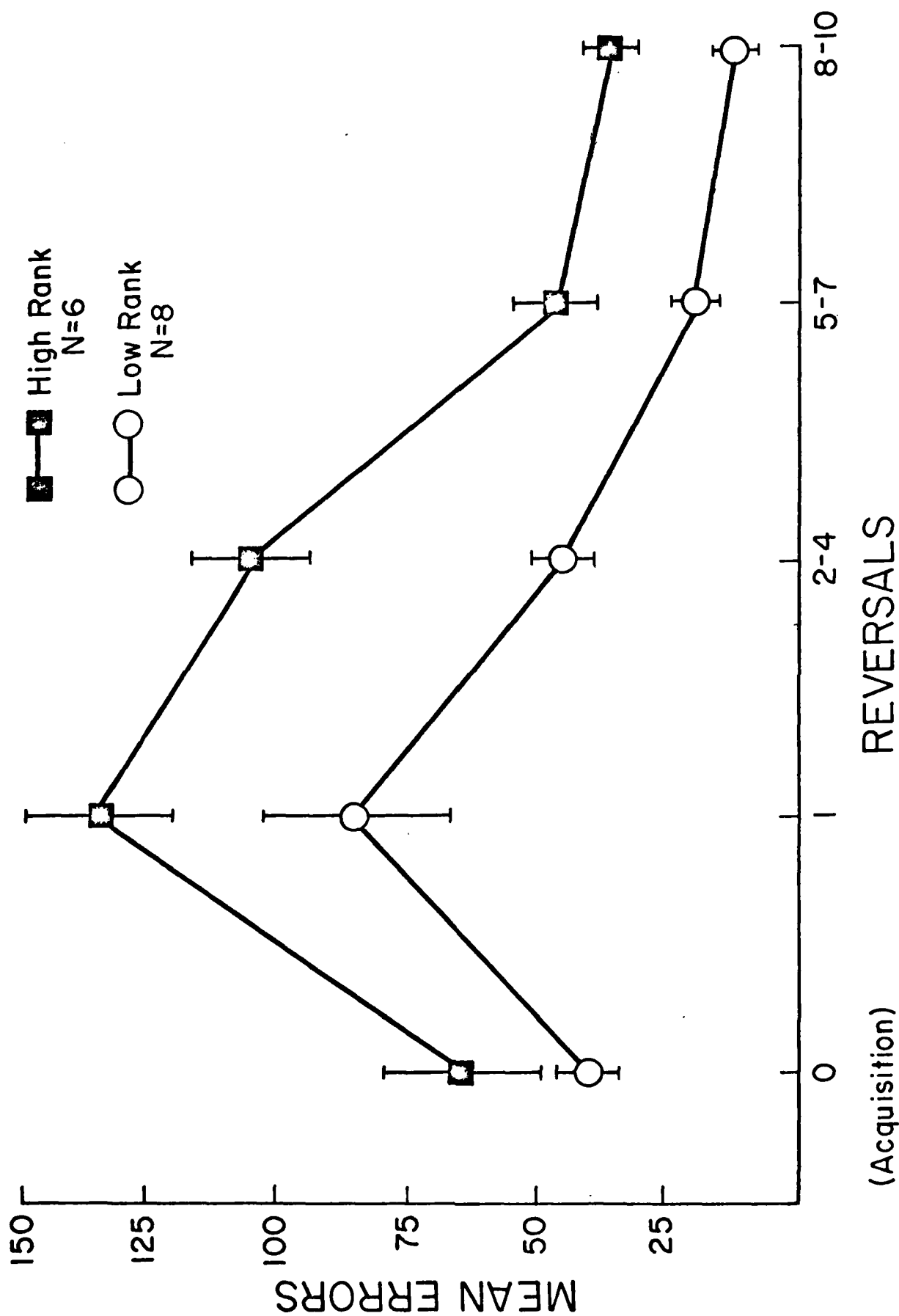
Figure 1. Mean errors to criterion on a brightness discrimination reversal task by high and low rank fascicularis.

The "efficiency" hypothesis was not supported; in fact, the results were just the opposite of what had been predicted. In interpreting these results, we suggested that the establishment and maintenance of high social rank outs an animal under chronic social pressure, the effect of which carries over to the laboratory testing situation and disrupts performance. If this were the case, one would expect that those animals that were most heavily involved in the social dynamics of the dominance structure of the troop during the testing of reversal performance would have been most seriously affected. With the exception of one adult male in T-Troop, the data fit this interpretation quite well. It was decided to test the animals on another complex problem solving task in the WGTA to test the robustness of the reversal learning findings and the viability of the "social pressure" hypothesis.

Social Behavior and the Reversal of Object Quality Learning Sets. In this study, the same WGTA and general procedures were used to test the same 17 males from T- and NT-Troops that had been used in the visual discrimination reversal learning study described in the last section. A large number of "junk" objects were used as discriminanda in training the animals on object quality learning set problems. The tasks followed the general procedures utilized by Meyer (1971) in his studies of habits and concept formation in rhesus monkeys. These procedures allowed the study of both habit formation, as represented by performance on intraproblem trials, and concept (learning set) formation as represented by interproblem performance on critical trials of both the object quality learning set and reversal learning set tasks. (The procedure has the additional advantage that, following extinction, it takes the animals about as long to relearn the reversal task as it did on initial acquisition. This means that manipulations of the dominance hierarchy can be made and the animals retrained to see if their rank changes are reflected in their performance).

The animals were first trained to criterion - 17 out of 20 correct trial two responses (85% correct) on a series of 6-trial and then 10-trial object quality learning set problems (The T-Troop monkeys were overtrained- they received 360 6-trial problems before starting the 10-trial problems). A 30 sec intertrial interval and a 30 sec maximum response time were used. The next stage of training involved reversals. In this condition, the monkeys were given four object quality learning set problems per test day with the problems being 8, 9, 10, or 11 trials in length. (The order of presentation of problems of different length was counterbalanced across days.) Reversals occurred on the fifth trial of the 8-trial problems, the sixth of the 9-trial problems, the seventh of the 10-trial problems and the eight of the 11-trial problems. When a reversal took place, the object that had been the correct stimulus up to that trial in the problem was no longer rewarded and the other object became the positive stimulus for the remaining trials of that problem. Criterion for this stage of the experiment was 17 out of 20 correct responses on the trial immediately following the first reversal trail.

The final stage of the study was the reversal extinction phase. This was similar to the reversal condition except that the correct stimulus was reversed for only one trial after which the original correct stimulus was again reinforced on the remainder of the trials of the problem. Criterion was 17 correct responses on the trial following the reversal trial over 20 consecutive problems.

As was done in the visual discrimination reversal study, the animals
in the top three ranks of the hierarchy of each troop were compared with the
remaining animals at each stage of the experiment. Testing each animal took
many months and it was not possible to test all of the animals at the same time.
Over the course of the entire study, there were a number of changes in the
social ranks of the animals. Each animal's rank at the time he was in a par-
ticular stage of training or testing was used in the analysis. As a result,
the performance of a single animal was sometimes included in the high rank
group and sometimes in the low rank group depending upon his rank during a
particular stage of the experimental testing.

Table 16 gives the number of trial-2 (6-and 10-trial problems) and
critical trial (reversal and reversal extinction problems) to criterion for
all four stages of WGTA testing. Because some animals shifted back and forth
between the high and low rank conditions, it was not possible to do an overall
repeated measures analysis of variance. Separate analyses of each stage, using
t-tests, showed that the difference in mean errors on trial-two performance on
the 6-trial problems was not significant. The large difference between high
and low rank conditions on the 10-trial problems was due to the performance
of NT-Troop males entirely. The T-Troop males, which had considerable over-
training, transfered their training from the 6- to the 10-trial problems
almost perfectly and there were no differences in the performance of high and
low ranking T-Troop males on this stage. The high rank group made significantly
more errors on critical trials on both the reversal learning and reversal
extinction stages than did the low rank group. It was also found that each
individual's performance on extinction was largely independent of its per-
formance on reversal acquisition.

Analysis of the total number of errors across all trials made in reaching
criterion on the 6-trial problems revealed that the animals in the high rank
group made significantly more errors per problem than the low rank group.
Thus, in relation to Meyer's (1971) definitions of habits and constructs, the
high ranking animals, which learned to discriminate the correct from the in-
correct object of a pair more slow'v, formed discrimination habits more slowly
than the other animals. However, as Table 16 shows, there was no difference
between the high and low rank groups in trial-2 performance across problems,
indicating that the animals in both groups learned the concept, defined in
human terms as a "win-stay/lose-shift" strategy with equal efficiency. In
fact, though it may have been coincidental, the two alpha males, Easy from T-
Troop and Ian from NT-Troop, reached criterion after only 35 and 54 problems,
respectively; these were the best performances of all of the animals tested.
Additional details on the procedures and results of this experiment may be
found in the published report (Bunnell and Perkins, 1980).

From late in 1978 through 1979, we retested 15 males on the object quality
reversal task and tested five additional animals from NT- and I-Troops. We
had expected, on the basis of Meyer's findings, that it would take animals
about as long to learn the reversal task following extinction as it had the
first time through. This turned out to be the case only for the 6 males in
T-Troop. Overall, the NT- and I-Troop males did much better then they did the
first time. The higher ranking animals within each troop tended to acquire
the reversal concept more slowly than lower ranking animals in that troop,
but there was considerable overlap between the scores of the low ranking animals
in T-Troop and the high ranking animals in NT- and I-Troops and the combined
scores for high and low ranking animals across troops did not differ significantly.

Table 16

Mean Trial-2 (Stages I & II) and Critical Trial (Stages III & IV)
Errors to Criterion by High and Low Ranking M. fascicularis*

| STAGE: | I | II | III | IV |
	6-Trial Problems	10-Trial Problems	Reversal Problems	Extinction Problems
HIGH RANK	X̄ = 47.20	X̄ = 26.33	X̄ = 50.43	X̄ = 96.25
	N = 5	N = 6	N = 7	N = 4
LOW RANK	X̄ = 38.75	X̄ = 7.00	X̄ = 17.44	X̄ = 48.54
	N = 12	N = 11	N = 9	N = 11

*One animal did not complete reversal learning and two did not complete
reversal extinction.

We're not certain, but we are inclined to attribute the differences in the troops' performance to differences in the animal's reactions to the different experimenters who ran the tests during this replication. The appearance of the expected relationship within troops despite several changes in rank within troops and the formation of a new troop was encouraging.

The experiments involving the reversal learning tasks provide additional support for the idea that social status is an important determinant of performance, but do not provide much insight into the mechanism that mediates the relationship between rank and performance. Clearly, there is no inherent negative relationship between some hypothetical generalized learning ability and social rank. In the first place, high ranking animals are quite capable of solving complex problems as well or better than low ranking animals as was shown by the results on the 6-trial object quality learning set task. Second, while it may be true that certain combinations of traits and abilities may predispose animals toward high social rank and that one might expect to find relationships between such traits and abilities and performance in nonsocial situations, changes in rank were quite frequent and performance seems to follow these changes quite reliably. It appears that the current social status of an animal affects current performance on at least some aspects of the WGTA tasks. Clues as to the nature of the processes involved are not readily discernable from an examination of the animals' response patterns. High ranking animals did not exhibit object perseveration or an inability to withold responses to the formerly correct stimulus after they had been reversed. The only difference between high and low ranking groups was that the former tended to distribute their response patterns more evenly across the eight patterns possible than did the low ranking animals. After giving up their old, correct, response pattern, they had more difficulty settling on the correct new strategy. Changes in the requirements of a task, as occur when the animals are given a reversal, or reversal extinction condition, are dealt with less efficiently by high ranking animals. Somehow, the business of establishing and maintaining high social rank carries over into the laboratory testing situation. Perhaps the high ranking animal is less attentive to the stimulus conditions and requirements of the task; perhaps the task is less meaningful to him either in terms of the rewards received or in terms of his perceptions of the consequences of his own actions. One way to examine this would be to try to manipulate the social dynamics of a group in order to vary the "social pressure" on the animals independently of rank to see what happens to performance. More will be said about this in the concluding section of this report.

Responses to Open Field Exposure and to Novel Stimuli in M. fascicularis.

The tendencies toward response bursting and the poorer performance on complex problem solving tasks by high ranking males suggested that there might be an emotional component associated with the stresses and strains of establishing and maintaining high rank that would make them more susceptible to changes in the response contingencies of a laboratory task, such as the omission of a reward or the reversal of positive and negative cues. To examine this possibility, the animals were tested in an open field situation and in the same field in the presence of familiar and unfamiliar stimuli. Tests were also conducted where a strange animal was placed in the field and with pairs of animals, with the pairs being selected on the basis of the amount and kind of social interactions they exhibited in the troop.

All of these tests were conducted in a square open field, 3.66 m on a side and 1.83 m high, situated in a large room inside the laboratory. The walls, constructed of asbestos cement board, and the concrete floor were painted white. The floor was divided into 16 equal squares by a painted grid. Five threaded studs, one in the center and the other four arranged in a square equidistant from the center and the walls, were embedded in the floor. These were used to attach the novel objects used in some of the tests. The open field was covered by 2 in chain link fencing and illuminated by four 150 watt floodlights suspended over the fencing. Two guillotine doors, located in diagonally opposite corners, served as entrances and exits for the animals. An elevated platform, located behind one wall of the arena served as the observers' station. It was shielded from the animals view by curtains and a large one way mirror. A keyboard and clock, connected to a PDP-8 laboratory computer, were used to record behavioral observations.

For each series of tests, the animals were run for a varying number of days, depending upon the nature of the problem. The basic procedure was to bring each animal to the field in a transport cage, open the guillotine door, and allow the animals a maximum of 15 min to "emerge" into the open field. An animal was said to have emerged when it entered the open field and moved one square beyond the entrance - a distance of .92 meters. When the animal emerged, the guillotine door was closed behind it and the behavior of the monkey was recorded for the next five minutes. At the end of five min the guillotine door was opened and the latency of the animals return to the transport cage, together with all behavior during this period, were recorded. In a test situation with a bare open field, then, the following events were recorded:

(1) Head Out Latency: Time from opening of the guillotine door until the animal puts his head through the door into the arena. (max. 900 sec).
(2) Body Out Latency: Time from the opening of the guillotine door until the animal enters the first square of the field. (max. 900 sec).
(3) Number of Returns: Number of times the animal reenters the transport cage after entering the first square ("body out").
(4) Emergence Latency: Time from opening of the guillotine door until the moves post the first square into the field. (max. 900 sec).
(5) Exploratory Moves: Number of squares traversed during the five min test period following emergence.
(6) Return Latency: Time from the reopening of the guillotine door at the end of the five min test until the monkey reenters the transport cage.
(7) Return Moves: Number of squares traversed during the return latency period.

The time spent on the floor of the field was differentiated from the time spent hanging from and moving about the ceiling.

When novel objects were present, the frequencies of the following additional behaviors were recorded:

(8) Lip Smack
(9) Orientations to object(s)
(10) Manipulations of object(s)
(11) Threats directed toward object(s)
(12) Bites object(s)
(13) Other contacts with object(s)

(14) Vocalizations
(15) Self-directed Behaviors (grooms, masturbates, etc.)

When other animals were in the field, social behaviors as listed in Table 7, were also scored.

Following a series of pilot studies conducted in January and February, 1977, the 9 males in T-Troop and the 12 males in NT-Troop that were serving as subjects in the operant studies were tested for five days in the empty open field. T-Troop animals were tested the first week of March, NT-Troop males were broken up into two squads. The first squad, containing the six oldest adult males, was tested during the second week of March, 1977. Because of scheduling problems, the second NT-Troop squad, containing the younger adults and the subadults, was tested for two days during the third week and three days during the fourth week of March, 1977.

There was a statistically significant rank order correlation of +.81 between high social rank and the number of squares traversed during the five minutes in the open field and high social rank for the nine males from T-Troop. Median emergence latencies were not related to rank when all nine animals were included in the analysis. However, if only the six top ranking animals were considered, the correlation between high rank and short emergence latency was +.97. In NT-Troop, the relationship between high rank and squares traversed appeared only among the five oldest and highest ranking animals in the first squad. There was no relationship between emergency latency and rank in the NT-Troop males.

In January, 1978, the same males were retested in the bare open field for three consecutive days using the same procedures employed in the first study. Three of the T-Troop males did not meet the emergence criterion on any of the three test days. Two of the NT-Troop males did not emerge on two of the test days and three more failed to emerge on one test day. From the data that were obtained, however, there was no evidence of the relationships between rank and movement in the open field that were seen in the first study.

In the next experiment, conducted in February, 1978, a stuffed teddy bear @ .33 m long by .25 m high was attached to the center stud of the open field. The stuffed toy was mounted on a platform with wheels so that the toy would spin when touched with any force. The animals were each tested for three consecutive days. One animal in T-Troop did not emerge on any day and two from NT-Troop failed to emerge on one test day. There was no relationship between either emergence latency or number of exploratory moves and social rank in either troop. NT-Troop males interacted with the stimulus object much more than did T-Troop males. In neither troop was there any relationship between social variables and the frequency of either contact or noncontact interactions with the stuffed toy. The presence of the novel stimulus object increased the emergence latencies of some, but not all, of the animals. Once again, there was no relationship between social rank and the magnitude or direction of emergence latency changes across the two experiments.

Because we were having difficulty getting some animals to enter the open field, the animals were given three days of training in which they received a reward of fruit for entering the open field. This took place in late May and early June of 1978. The animals were not tested again in the open field until February of 1979, well after I-Troop had been formed and its social structure stabilized.

The next experiment involved the males of all three troops. Four stimulus objects were attached to the peripheral studs in the floor of the field. The position of the objects in the field was changed on each of three habituation training days. On the fourth day, one of the stimulus objects was replaced by a novel object. This was always placed on the stud closest to the guillotine door so that it faced the animal when the trial began.

The results were disappointing. One animal in each troop failed to emerge on any of the four days. One animal in T-Troop did not emerge on the day the novel object was presented and another animal in T-Troop did not emerge during the first three habituation trials, but did enter the field on the day the novel stimulus was presented. There were no significant correlations between any of the open field measures and any of the social variables. The study was replicated, using the I-Troop males and a new novel stimulus, in late August and early September, 1979. Once again there was no relationship between open field scores and social variables.

In July, 1980, all of the males in the three troops were tested again. This time they were given three days of exposure to the empty open field followed by a fourth day in which an adult male, which none of the animals had ever seen before, was placed in a cage placed in the center of the field. There were statistically significant correlations between high social rank and mean exploratory moves for the three days of bare field testing (+.90) and on the day the strange animal was introduced (+.81) for the eight animals then in I-Troop. However, there were no significant correlations between any social variables and any open field measures in T- and NT-Troops. Two of the NT-Troop males and one from T-Troop did not emerge on two of the three tests with the field empty. One T-Troop male did not emerge on any of the four days and one NT-Troop male did not emerge on the day the strange animal was placed in the field. Even when the data of these animals were discounted, no relationships emerged between the variables of interest.

The next study, conducted in July and August, 1980, was done with al ɔr the I-Troop males except Alabama, who had been removed from the troop for a social manipulation. Grandpa, the stimulus male from the preceding study, was also included (he would be introduced into I-Troop immediately after testing in the pairs situation used in this study). There was a total of 8 monkeys in the experiment. The animals were tested in pairs. Each animal was paired with three other animals from the troop, or with two and Grandpa, during the course of the study. The first set of pairings was done on the basis of alliances between animals in the troop. Pairs were chosen in which the two animals exhibited consie able nonagonistic social behavior toward each other. The other two sets of pairings used animals where there was considerable agonistic behavior between members of the pair. Pairings with Grandpa were used to observe reactions to an animal which was not a member of the group.

In testing the animals, one member of the pair was released into the field. Two minutes later the other animal in the pair was allowed to enter the arena. The behavior of the second animal was scored throughout the test; measures included latencies, exploratory moves, and social behaviors. (Only the emergence latency of the first animal was recorded.) On the second day, the same pairs were used, but the order of the release of each monkey was reversed. On the third day, all animals were tested in an empty field. On days 4, 5 and 6, the tests were repeated. On days 7 and 8, new pairs were used and each animal was released as both the first and second animal of pairs. On days 9 and 10, more new pairs were formed and the procedure repeated once again.

There was no relationship between behavior in the empty field and any social variable. There was a positive correlation of borderline significance between high social rank and number of exploratory moves made after release into the field in the presence of another, known, animal. Excluding the pairing of Yamamoto and Grandpa in the first set of pairings, the rank order correlation was +.79. For the other pairings, with Grandpa's partner excluded, the correlations were +.66 and +.71. A two-tailed t-test yields a p between .10 and .05 for these rhos.

Emergence time tended to be much longer when an animal was the second animal released in a pair then when that animal was released into an empty field, either by being released first, or on days when pairs were not tested. Emergence time varied considerably within the same animal, depending upon which of the other troop members was present in the field when he was released. However, there was no apparent relationship between the social behavior of a pair and emergence time. Very few agonistic interactions took place in any of the pairs.

At the time the project was ending, one final three day test was conducted in the empty open field, using the males from all three troops. The nine males in I-Troop, with Alabama returned to the group and Quotation added, exhibited a significant correlation of +.74 between rank and exploratory moves. However, there was no evidence for the presence of such a relationship among the five males in T-Troop or the six from NT-Troop that were tested.

Correlations between open field behavior and other laboratory tests, including operant testing and WGTA testing, were generally low and non-significant. Because operant testing frequently had to be suspended on the days when open field testing was conducted, the data could not be used for examining day-to-day relationships between the various tasks.

Overall, the animals appeared to behave in highly idiosyncratic ways in the open field tests. These individual patterns of responding carried across test conditions and tended to submerge what few, if any, relationships between social and open field variables that might have been present. It is probably safe to conclude that the occasional significant relationships obtained between social rank and exploratory behavior resulted from changes in the rank structure of the groups such that rank temporarily corresponded with exploratory tendencies. The use of the paired tests did produce some interesting changes in the behavior of the monkeys but it is not clear that these added anything that could not be seen while observing the interactions of the same pairs within the context of the group situation.

Social Behavior and Observations of Crab-Eating Macaque Groups.[3]

The observations of social behavior in the fascicularis groups were made using the behavior inventory presented earlier in Table 7. Because of limitations on the size of the matrices that could be constructed to summarize the dyadic interactions between animals, data were obtained only for the 24 oldest animals in T- and NT-Troops during most of the project. However, during the last 24 months of the project when the use of focal animal observation techniques was increased, procedures were modified to enable us to include observations of infants and the younger juveniles in the observations.

The age/sex ratios in the fascicularis troops at the beginning of the work with these groups in the winter of 1975 and again at the end of the project in the fall of 1980 are shown in Table 17. Three adult males were added to T-Troop in the fall and winter of 1975-76 and one additional adult male was placed in NT-Troop in the winter of 1976. By April of 1978, the age/ sex ratios of both troops had altered considerably and no longer approximated that described for groups found in the wild (Angst, 1975). This was due both to unexpectedly high mortality among females of all ages as well as a disproportionately high ratio of male to female births prior to and during the first three years of the project. As a result, there were too many adult males and too few females of all ages. In April of 1978, a total of nine males, seven adults and two subadults, were removed from the two parent troops in order to restore a more natural balance to the age/sex ratios in these troops. The nine males were used to establish a third, all male troop, called I-Troop.

Observations.

The observations of social behavior (usually one hour per group, five times a week, weather permitting) were scheduled in accordance with the laboratory tests being conducted with the animals. During fall, winter, and spring, the observations were usually made immediately after the males were returned to the compounds following testing in the laboratory normally between 1100 and 1400 hours. In the hot summer months, observations were usually made in the morning prior to 1000 hours before the males were removed from the groups for laboratory testing. At times, scheduling contingencies required that observations be made during the late afternoon or early evening in the summer. In all cases, we attempted to observe the troops when social activity was at its highest during each day.

Each troop was housed in its own compound, identical to that described earlier for the rhesus group. In recording social behavior, either one or two observers entered the observation chamber in the compound, the troop

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[3]The social behavior of the rhesus monkeys used in this project has been described in detail in the section of this report dealing with operant behavior and will not be repeated here.

Table 17

Social Group Composition of M. fascicularis Troops
Winter 1975 and Fall 1980

	Troop	Adult M	Adult F	Subadult M	Subadult F	Juvenile M	Juvenile F	Infant M	Infant F
1975	"T"	6	10	4	-	2	7	3	1
	"NT"	6	5	5	-	3	5	5	1
1980	"T"	7	12	3	-	2	2	3	3
	"NT"	8	10	4	-	2	4	2	3
	"J"	10	-						

was restricted to the compound area by closing the guillotine door to the runway, and social behavior was recorded for one hour. Data were either punched directly onto paper tape using an octal keyboard, or were written sequentially by hand and later transcribed using the keyboard-tape punch system. (In the latter case, accurate latency and duration information were not obtained.) When a group scan observation procedure was used, an attempt was made to record all of the social behavior of the 24 oldest monkeys in the troop, with priority being given to interactions which involved the males of the troop that were undergoing testing in the laboratory. When a focal animal observation technique was used, the behaviors performed or received by a particular animal (the "focal" animal) were recorded exclusively for a predetermined period of time, usually five minutes. Usually all of the males undergoing laboratory testing in a troop would be the focal animals once or twice during a single observation period.

In collecting social data, the observers would record the code for the animal exhibiting a behavior, the code for the behavior itself, and then the code for the animal receiving the behavior if the behavior was a social behavior. The tape punch system automatically entered the time of occurrance of each entry as well as the keyboard identification. Thus frequency, latency, duration, and response sequence information were available from the data tapes. Frequency and sequence data were used extensively in analyzing the social behavior of our groups; latency and duration data were used less frequently - primarily in conjunction with the study of affiliative behavior described at the end of this section.

Analysis.

As we have noted earlier, social rank is determined by defeats. The occurrence in any animal of a submissive behavior indicates that that animal is inferior in rank to the animal toward which the submissive signal is directed. It is important to recognize that the means by which one animal establishes and maintains dominance over another (e.g., by physical attack, threat, teaming up with or being protected by another animal, etc.) can vary from animal to animal, from group to group, and from situation to situation. Only by recording and analyzing all of the data of all of the animals can we define both the behavioral constancies and the range of variation that are present in each group. This provides a more sophisticated assessment of social status and social organization than does the simple assignment of social rank to individuals.

In analyzing each day's observations, the laboratory computer provides a summary which gave:

1. A listing of the number of behaviors recorded for each animal and a listing of the frequency of occurrence of each behavior during that observation period.
2. A listing of the frequency with which each animal exhibited each behavior during the observation period.
3. A listing of the frequency with which each behavior exhibited by a given animal was directed toward each of the other animals in the troop.

These listings were used to monitor day-to-day interactions in each group
and to pinpoint changes in the relationships between individuals. Then a
summary of the intragroup relationships was obtained by combining several days'
data in a matrix analysis. In this procedure, the computer went through all
of the data and determined the social rank of each animal on the basis of who
was defeated by whom, using the submissive behaviors listed in Table 7. It
then printed a series of six matrices, utilizing the same rank order -- the
dominance hierarchy -- that it determined from the analysis of the submission
data. In each matrix, the frequency of occurrence of each behavior, or class
of behaviors selected for inclusion in that matrix is given for each animal
with respect to every other animal in the group. Typically, four of the
matrices were used to summarize the combinations of behaviors listed in the
functional categories of Aggressive, Submissive, Sexual, and Other Social of
Table 7. For the other two matrices, any individual behavior of interest
might be selected. Most our analyses involved grooms and sit-next-to from
within the Other Social functional category; however, matrices for play or
for distinguishing between contact and noncontact aggression were also
utilized. Additional analyses allowed us to determine the frequencies with
which particular behaviors, or categories of behavior, were directed toward
or received from selected age/sex classes by each of the males in the group.

Examples of three of the functional category (primary) and one single
behavior (secondary) matrices are given in Table 18. Here, social data
obtained from observations of I-Troop during August, 1979, using the group
scan technique, are presented for submissive, aggressive, other social,
and grooming behaviors. Reading a matrix horizontally, across columns, gives
the number of times each animal "does" the behavior to each of the other animals
in the troop. Reading vertically, across rows, gives the number of times
each animal "receives" the behavior from each of the other animals. Thus,
Alabama submitted to Gus, the top-ranked, or alpha, animal 13 times during
the month, but did not submit to any other animal. The dominance structure
of the group is linear and clear for the first five ranks in the group.
It is less clear for the four lowest ranking animals where Equal, who other-
wise would be tied with Daque for fifth rank, is marginally subordinate to
Yuk and the relationship between Yuk and Yamamoto is unresolved.

The other three matrices of Table 18 utilize the same rank order as the
Submissive matrix. The second matrix, for Aggressive behavior, shows that
high ranking animals are not necessarily the most aggressive monkeys in the
group. Matrix 3, for Other Social behavior, contains social grooming behavior
within it. Grooming has been broken out of the third matrix and used to
construct a secondary matrix for Grooms, Matrix 4.

The computer was programmed to remember the social rank of each animal in
each group. It began each analysis of a new set of observations with the rank
structure it had determined from the most recent preceding analysis. Thus, if
no submissive behavior was seen between a pair of animals in the new set of
observations, the dominance/submission relationship between those animals was
assumed to be unchanged from the last time they had engaged in an agonistic
interaction in which one had submitted to the other.

Table 18

PRIMARY (1,2,3) and SECONDARY (4) SOCIAL MATRICES
I-TROOP   7/30-8/31/79   19 DAYS-GROUP SCAN

1. SUBMISSIVE:

	GUS	ALA.	SPI.	CRA.	DAQ.	EQU.	NOD	YUK	YAM.	SUM:
GUS	-	3	1	1						5
ALABAMA	13	-								13
SPIRO	24	8	-							32
CRACKER	5	36	9	-						50
DAQUE	11	8	8		-		2			29
EQUAL	22	16	23				1	6		68
NOD	10	18	5		11	2	-	2		48
YUK	8	4	4	39	18	5	4	-	1	83
YAMAMOTO	23	12	12	3	5	2	5	1	-	63
TOTALS:	116	105	62	43	34	9	12	9	1	391

2. AGGRESSIVE:

	GUS	ALA.	SPI.	CRA.	DAQ.	EQU.	NOD	YUK	YAM.	SUM:
GUS	-	1			2		1		1	5
ALABAMA		-	3	4		3	4		3	17
SPIRO			-	9	7	17	3	2	3	41
CRACKER				-	5			62	4	71
DAQUE					-		19	23	5	47
EQUAL	2		3	1		-	9	17	4	36
NOD	1	1		2	23	10	-	16	5	58
YUK						14	8	-	3	25
YAMAMOTO				1	2	4	4	1	-	12
TOTALS:	3	2	6	17	39	48	48	121	28	312

3. SOCIAL:

	GUS	ALA.	SPI.	CRA.	DAQ.	EQU.	NOD	YUK	YAM.	SUM:
GUS	-	33	19	3	7	13	6	14	17	112
ALABAMA	8	-	3	2	11	23	12	5	22	86
SPIRO	12	1	-	2	7	16	32	17	27	114
CRACKER	1	1	1	-	2	12	12	39	29	97
DAQUE	14	5	30		-	10	12		2	73
EQUAL	10	7	26	26	10	-	16	13	7	115
NOD	5	1	14	13	5	4	-	7	26	75
YUK	6	3	4	18		11	10	-	4	56
YAMAMOTO	20	10	14	63	2	4	40	6	-	159
TOTALS:	76	61	111	127	44	93	140	101	134	887

4. GROOMS:

	GUS	ALA.	SPI.	CRA.	DAQ.	EQU.	NOD	YUK	YAM.	SUM:
GUS	-	13	8			1		5	1	28
ALABAMA	1	-			1				1	3
SPIRO	4		-	1		6	12	6	12	41
CRACKER				-	1	2	2	10	14	29
DAQUE	5		15		-	2	3		1	26
EQUAL	5	1	10	9	2	-	5	6	2	40
NOD	1		6	1	1		-	2	3	14
YUK			1	9			2	-	1	13
YAMAMOTO	8	1	4	15			3		-	31
TOTALS:	24	15	44	35	5	11	27	29	35	225

The number of observation periods that were incorporated into each analysis of social behavior varied depending upon circumstances and the needs of the project with regard both to social questions and to the laboratory experiments in progress at the time. In almost all cases, a monthly summary, covering 4 or 5 weeks of observations, was obtained for each troop. In a few instances most frequently during the winter when cold, wet weather reduced social activity considerably, longer periods of time were combined in the summary analyses. If a significant shift in interanimal relationships showed up between one month and the next, day-by-day and week-by-week matrices were used to pinpoint the time when the changes took place and to elucidate the nature of the altered social structure.

Matrices covering longer periods of time -- from several months to a year -- were also obtained and used in the initial study of affiliative behavior that will be described later in this section.

Finally, we often made experimental manipulations of the social structure and composition of the troops by introducing new animals, removing and replacing troop members, etc. Separate sets of social matrices were computed for the periods prior to, during, and following such manipulations.

Social Changes.

Changes in the composition and social organization of the monkey troops took place throughout the project. Some of these changes were spontaneous; others were the result of experimental intervention. Spontaneous changes in social behavior and organization frequently followed the changes in group composition that resulted from the death of an animal or, more rarely, the birth of an infant. On occasion, animals had to be removed from the troops for treatment of disease or injuries. When this happened, the animal was often held out of the group for an extended period of time in order to study the effects of the absence of that animal on social behavior. (Usually, removing an animal for two or three days had very little effect on the social structure and when the animal was placed back in the group it would immediately assume its previously held rank, with little or no agonistic interactions taking place. One, two, or more weeks were generally required before substantial changes became apparent.) Other spontaneous changes resulted from agonistic interactions within the troops.

Experimental manipulations were performed in several ways. First, there were the removals and replacements that utilized a procedure that was similar in many respects to the removal and replacement of sick or injured animals that was described in the preceding paragraph. An animal was chosen for removal on the basis of some characteristic such as rank, aggressiveness, alliance with another animal in the group, kinship, etc. It would then be removed from the group and the social behavior observed for signs of changes in behavior and/or social organization. After the behavior of the group had stabilized in the absence of the monkey that had been removed, that animal was reintroduced into the troop. When an animal was reintroduced, social behavior was recorded for several hours on the day of the introduction and no laboratory testing was done for 24 hours after the introduction took place. Data from the introduction were analyzed separately from the data

obtained for the days preceding and the days following the manipulation.
On three occasions animals were removed from one troop and introduced into
a differen. troop and new unfamiliar animals were introduced into the troops
on five occasions.[4]

Finally, a new group was formed during the course of the project by
putting together surplus males from T- and NT-Troops to form I-Troop.
Three adult and two subadult males that had been removed from T-Troop for
one month were put together with three adult males from NT-Troop that had
also been isolated for a month. Following this simultaneous introduction
and the stabilization of the social structure of the new group, an adult
male from T-Troop and one from NT-Troop were introduced into I-Troop at
two week intervals.

Results.

During the first two years of social observations on T- and NT-Troops,
from the late winter of 1975 through the spring of 1977, we concentrated on
male social rank and male response frequencies within the agonistic behavior
categories in our search for relationships between social variables and
performance measures. It was obvious that the male social hierarchy was
a key factor in the social organization of the troops and played an important
role in the expression of both agonistic and nonagonistic behaviors among all
members of the groups. However, the emphasis on the male hierarchy and the
agonistic behaviors associated with the establishment and maintenance of
the hierarchy did not necessarily provide enough information for a thorough
understanding of the social behavior and organization of the groups.

The dynamics of the social organization of T- and NT-Troops were
different at different times. During the first year of observations, the
structure of T-Troop was quite stable. Once the initial hierarchy was es-
tablished, it changed very little and the amount of agonistic behavior was
quite low. The introduction of three new animals into the troop produced
flurries of agonistic encounters, but the relative ranks among the males
that were original members of the group did not change. The new animals
were incorporated into the group without a great deal of disruption, even
though two of them established themselves as high ranking animals. In
contrast, during the same period of time, the relationships among the five
adult males then present in NT-Troop were very fluid and agonistic behavior
was much greater than in T-Troop. Each of the five adult males in NT-Troop
became the alpha male at some time during the first 15 months after the
group was first established. During 1976, agonistic activity and hierarchy

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[4] Four of the "new" animals had been members of the original Yerkes group from
which T and NT were formed. However, they had been separated from the other
animals for at least two years and from each other for at least one year
before these introductions. The fifth new animal had never been a part of
the original group.

changes increased gradually in T-Troop and declined in NT-Troop such that, by the spring of 1977, the social organization of T-Troop was relatively unstable in comparison to that of NT-Troop. These shifts made the task of comparing correlations between social variables and performance measures more difficult. It appeared that for some, but not all, of the laboratory tests we were using, significant relationships between social variables and performance scores were present only when the social organization was under tension as evidenced by high levels of agonistic behavior and by changes in the dominance hierarchy.

As noted earlier in this section, the means by which social rank is established and maintained can vary considerably across animals and groups of animals. Correlations between frequencies of aggressive behaviors and high rank are not uniformly high and positive. Because social rank was the one social variable that was most frequently associated with performance scores on laboratory tests, it was necessary to investigate the dynamics underlying the rank structures of the groups in some detail.

An example of one such analysis is given on the next page (Figure 2). To construct this figure, the data recorded in the Other Social category of the behavior inventory for NT-Troop for an entire year of observations has been subjected to a cluster analysis. A matrix, similar to Matrix 3 in Table 18, was constructed using all of the data obtained from 136 hours of group scan observations on NT-Troop from April 1976 through March 1977. The proportions of Other Social behavior initiated by and received from each animal were calculated using row and column totals of the matrix and converted to z scores (Fischer, 1977). The nonagonistic social relationships between the 24 oldest animals in the troop are diagrammed in the figure. The larger the relationship, the higher the z score and the thicker the line drawn to denote the relationship between the animals. The lower case "r"s associated with some of the arrows indicate kinship relationships. Males are identified by underlining their names.

Similar analyses were made of the data from 1975-76 for NT-Troop and for T-Troop for both years. Several generalizations emerged across both troops. Adult females tended to receive a considerable amount of non-agonistic social attention from their daughters. The reciprocated this attention only moderately, but tended to devote their nonagonistic social behaviors toward one or more of their adult sons in the troop and toward unrelated males with which they were sexually active. The adult sons reciprocated to some extent, but tended to direct their attention toward unrelated adult females if they were high ranking in the group and toward other males if they were not. Frequently there were strong, nonagonistic social relationships exhibited between low ranking brothers. In the spring of 1978, focal animal observations were made of 12 males and 8 females in NT-Troop. Cluster analyses of these data confirmed the generalizations obtained with the group scan procedures of the preceding two years.

Analyses of the agonistic interactions for 1975-76 and 1976-77 indicated that there was a dominance order in the matriarchies of both troops. In T-Troop, the dominant matriarchy was that of Quail, a female born in 1961.

CLUSTER ANALYSIS

NT-TROOP   1976-77
Nonagonistic Social Behavior
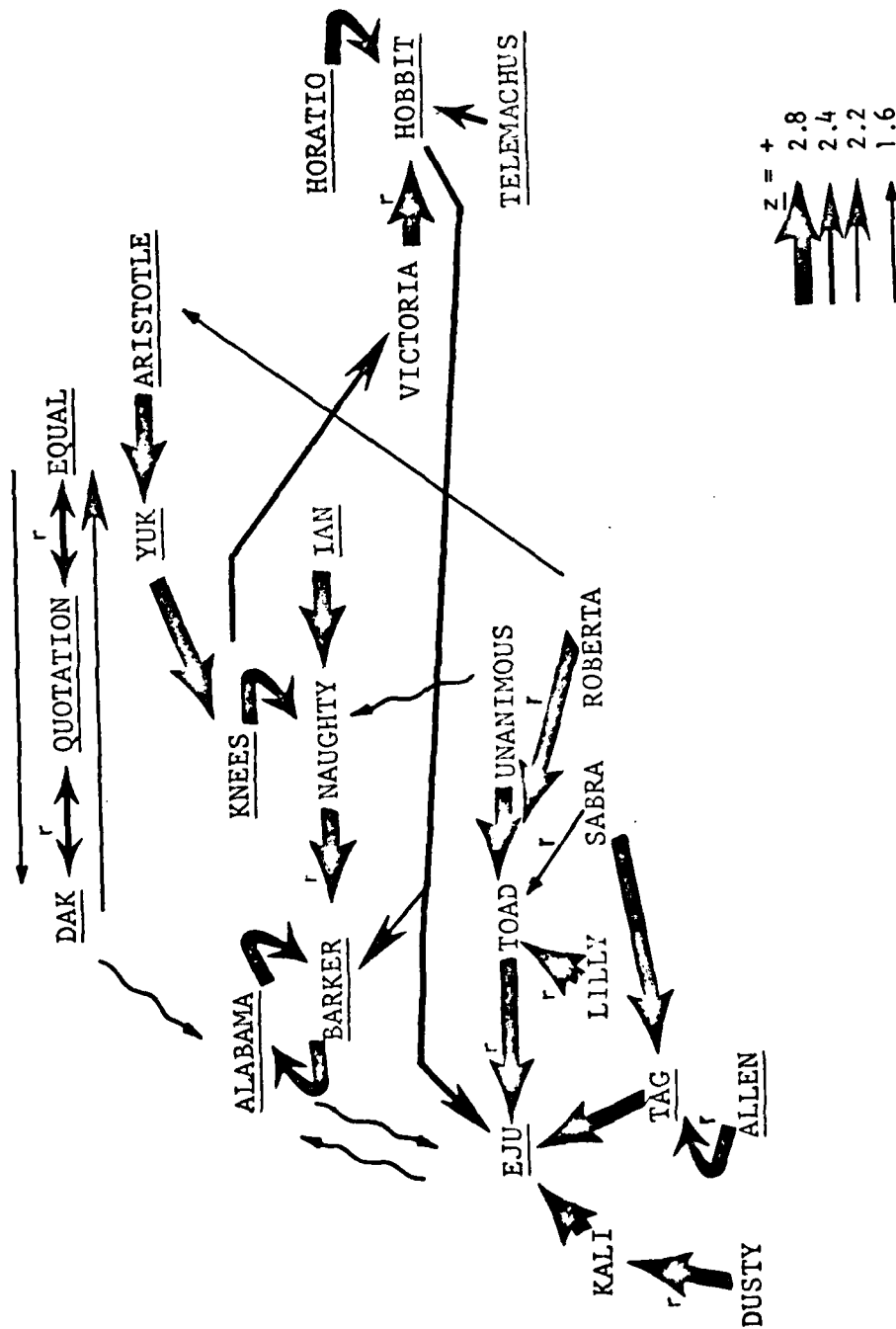(136 Hours - 8237 Events)

Figure 1. Analysis of nonagonistic social interactions. Names of males are underlined. The small "r"'s indicate kinship relationships.

Although Quail's matriarchy was dominant over that of the other three mat-
riarchies in T-Troop, she was not the highest ranking female in the group.
Instead, the top ranking female was Zelda, Quail's eldest daughter. In
NT-Troop Toad, the oldest female was the highest ranking female in the group
and her matriarchy was dominant until the fall of 1979. In February, 1976,
the second ranking matriarchy in NT-Troop lost its matriarch, Patsy. However,
her oldest daughter, Dusty, continued to dominate all of the females in all
of the matriarchies except Toad's and kept Patsy's matriarchy in second
place until the winter of 1980.

In 1979, the role of these matriarchies in the establishment and main-
tenance of the male dominance hierarchies was explored. Data from the
agonistic interactions observed in preceding years were examined. Little
could be learned from T-Troop, since the adult males that were high ranking
did not have living mothers in the group. Quail, the matriarch of the dominant
matriarchy, had only one adult son in the troop and he, Ralph, had neurological
problems and was never a factor in the male dominance hierarchy. In NT-Troop
however, Toad's son, Eju, and Naughty's son, Barker, were among the oldest
and most socially active males in the dominance hierarchy. One of Naughty's
sons, Telemachus, and two of Victoria's male offspring, Yuk and Hobbitt,
reached adulthood in the course of the project.

When a male was removed from a group and held out for several weeks, he
usually lost rank upon his return. Barker and Eju were exceptions to this
generalization, however, and it was thought that the presence of their mothers,
together with their matriarchies, might provide support which enabled them
to maintain a more constant status in the group than the other adult males.
Although all five of the oldest males in NT-Troop had been the alpha male
at some point during the first two years of the troop's existence, indicating
that the matriarch's presence was not essential to the achievement of high
rank, Barker's and Eju's ranks fluctuated less than did those of Knees, Ian,
and Alabama. Ian had been the alpha male in NT-Troop for more than 18
months when he was removed for 19 days in September of 1978. When he was
returned to the troop he was defeated by Eju. Eju continued to be subor-
dinate to Barker, however, and Barker and Eju ranked first and second,
respectively, until the fall of 1979. In late September, both Barker and
Toad were removed from the NT-Troop; Toad was returned after three weeks
and Barker was held out for four weeks. While both animals were out of the
group, Eju ranked first and was not challenged by any of the other adult
males. However, Toad's daughters Roberta and Lily were defeated by members
of other matriarchies in the troop during this period. Toad's return to the
troop did not produce any obvious alterations in group social organization --
she submitted only to her son Eju, was not at all aggressive, and interacted
primarily with her own sons and daughters. Barker's return was not accompanied
by very much aggressive activity. Both he and Eju showed some aggression
toward the other males in the troop, but not toward each other. It was
several days before Eju was observed submitting to Barker, indicating that
Barker was once again the alpha male in NT-Troop.

In late November, 1979, Naughty successfully challenged Toad and became the highest ranking female in the troop. Toad, whose adult daughters had been defeated in October, fell below Naughty, Victoria, Unanimous and Dusty in rank. Subsequent to Toad's defeat, Eju lost rank and came to rank below not only Barker, but Quotation, Weed, and Naughty and even, for a time, Ian as well.

Though by no means conclusive, the drop in rank by Eju subsequent to the defeat of Toad's matriarchy suggested that a better understanding of the social dynamics surrounding the matriarchies was important to a more complete understanding of the structure and organization of the group. To explore these factors more thoroughly, a full scale study of affiliative, as opposed to agonistic and sexual behaviors was conducted with T- and NT-Troops during the last year of the contract. This was a dissertation project by Mary Norris Perkins (Perkins, 1981) in which behaviors which tend to bring animals together and keep them together, such as the behaviors in the "Other Social" category of Table 7, were examined across the various age/sex classes of each troop.

In gathering the data for this study, each animal in the two troops, including the infants, was the subject of one five minute focal observation each week. In addition, group scan observations were conducted for 20 minutes before and after each day's focal sessions. In an observation cycle of one week, 8-10 animals were randomly selected, without replacement, for each day's focal sessions so that, at the end of four days, all of the animals in a troop had been the focal animal for one 5 minute observation. The fifth day of the work week was reserved for makeup session -- usually necessitated by bad weather -- or for one hour group scan observations. Two highly experienced observers, one for each troop, made the observations. Following several months of pilot work in which the behavior category definitions were refined and the observation procedures tested, the actual study was conducted from July 14 through December 2, 1980. There were several births and deaths in the two troops during this time and one subadult and one juvenile had to be removed from NT-Troop for about one week for treatment of an illness. In addition, Quotation, an adult that had become the alpha male in NT-Troop in April, 1980 was removed from the troop in August -- he was later placed in I-Troop -- and Knees, then a low ranking male in T-Troop was removed at the same time and returned 6 weeks later. With these exceptions, the troops were intact throughout the study. Overall, the majority of the animals were each observed for 17 focal observation periods. In addition, there were more than 60 hours of group scan observations of each troop during this same period.

1. Both troops exhibited large amounts of affiliative behavior. T-Troop members were involved in these behaviors during 82. of the observation time and NT-Troop members during 67 of the time.
2. The adult females were the primary affiliative force within each troop. They exhibited affiliative relationships not only among themselves, but also with male adults and male and female juveniles. The relationships between female adults and male and other female adults were characterized by reciprocal grooming, nonspecific body contact, and proximity. The juveniles did not reciprocate the grooming received from female adults, but were likely to be in nonspecific bodily contact and in proximity to adult females.

3. The affiliative relationships between adult females and juveniles were biased in favor of kinship.

4. Affiliative interactions between male adults were high in T-Troop where there was little intermale aggression and low in NT-Troop where the rate of aggression was four times greater than it was in T-Troop.

5. Male subadults tended to be an affiliative group within themselves. They also were involved in affiliative interactions with adult *and juvenile males*, but not with females of any age group.

6. The extreme playfulness of the juvenile males seemed to promote affiliation within the troops by bringing together juveniles and subadults. The adults in the two troops rarely, if ever, exhibited play behavior, however, no play was recorded by adults during the focal observation periods and, in 100 hours of group scan observations on each troop over a one year period preceding and including this study, there were only 3 instances of play between adult males in T-Troop and 9 instances in NT-Troop. One instance of play was recorded between an adult male and adult female in T-Troop during this time and no play was recorded between adult females in either troop. However, it is interesting to note that during this same period of time, there were 119 instances of play between adult males in the all male troop, I-Troop. This indicates that group composition is very important in determining the occurrence of play behavior and suggests that group dynamics may be quite different where females, and particularly adult females, are absent.

The primary affiliative interactions that took place in both troops are diagrammed in Figure 3 .

It is clear that the animals in both troops spent considerable time in nonagonistic, nonsexual social behavior and that the adult females were a major focal point of this type of activity.

The relationships between adult male social rank and nonagonistic, nonsexual social behavior were examined. This was done by computing rank order correlation coefficients between male social rank and the frequency of "other social" behaviors prior to and after the social manipulations made with T- and NT-Troops in August, 1980. For the period from April through July, 1980, the correlations were high and positive between adult male rank and the total frequency of these kinds of social behavior: rho = +.89 for T-Troop (n=6) and +.88 for NT-Troop. Following completion of the social manipulations these correlations were +.93 for T-Troop (from mid September through November) and +.81 for NT-Troop, where n=6 following the removal of Quotation and the death of Aristotle (from early August through November).

Correlations were also obtained between male rank and the amount of "other social" behavior each male directed toward each female with which he was sexually active during each month of the study. Again, the relationships were high and positive both before and after the social manipulations. The correlations for T-Troop were +.83 and +.81 for the two periods; for NT-Troop they were +.78 and +.91.
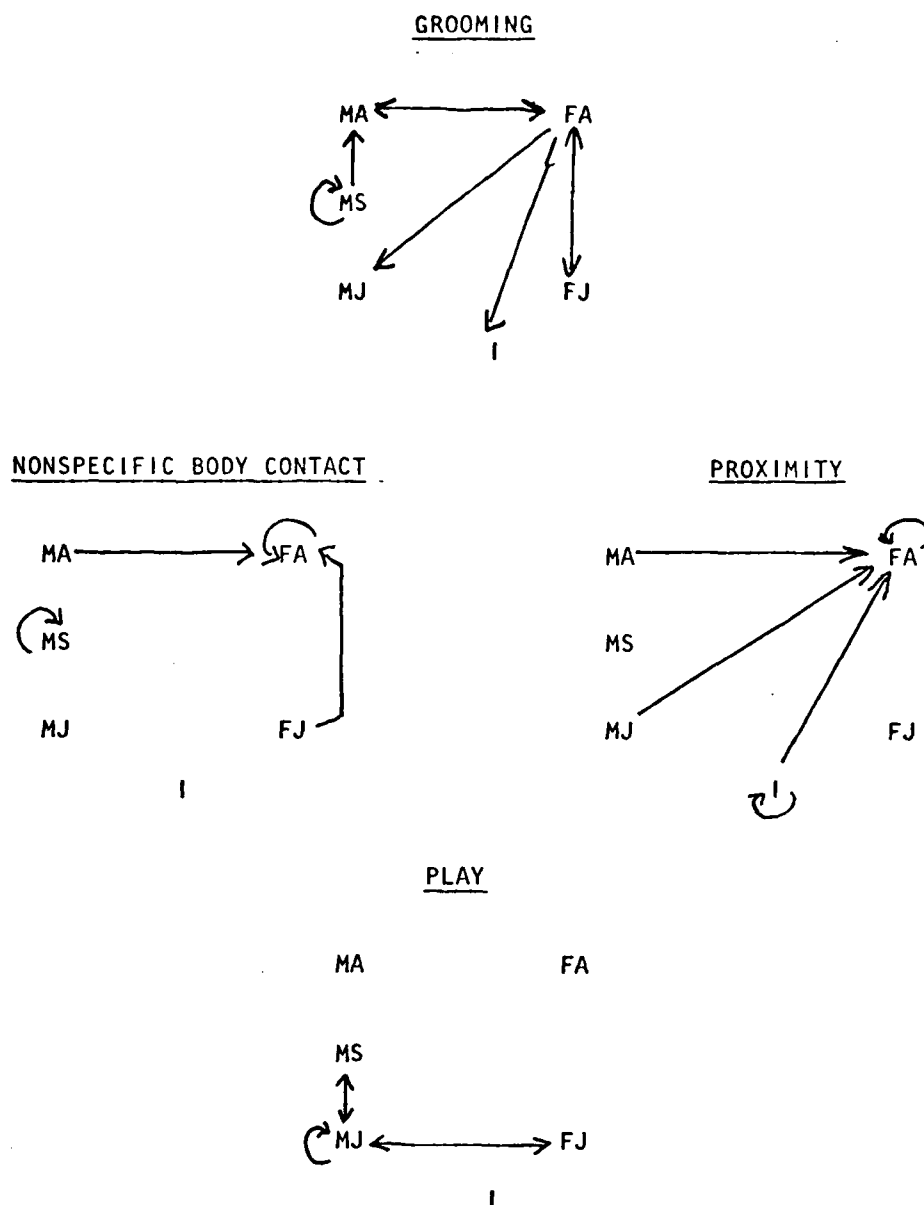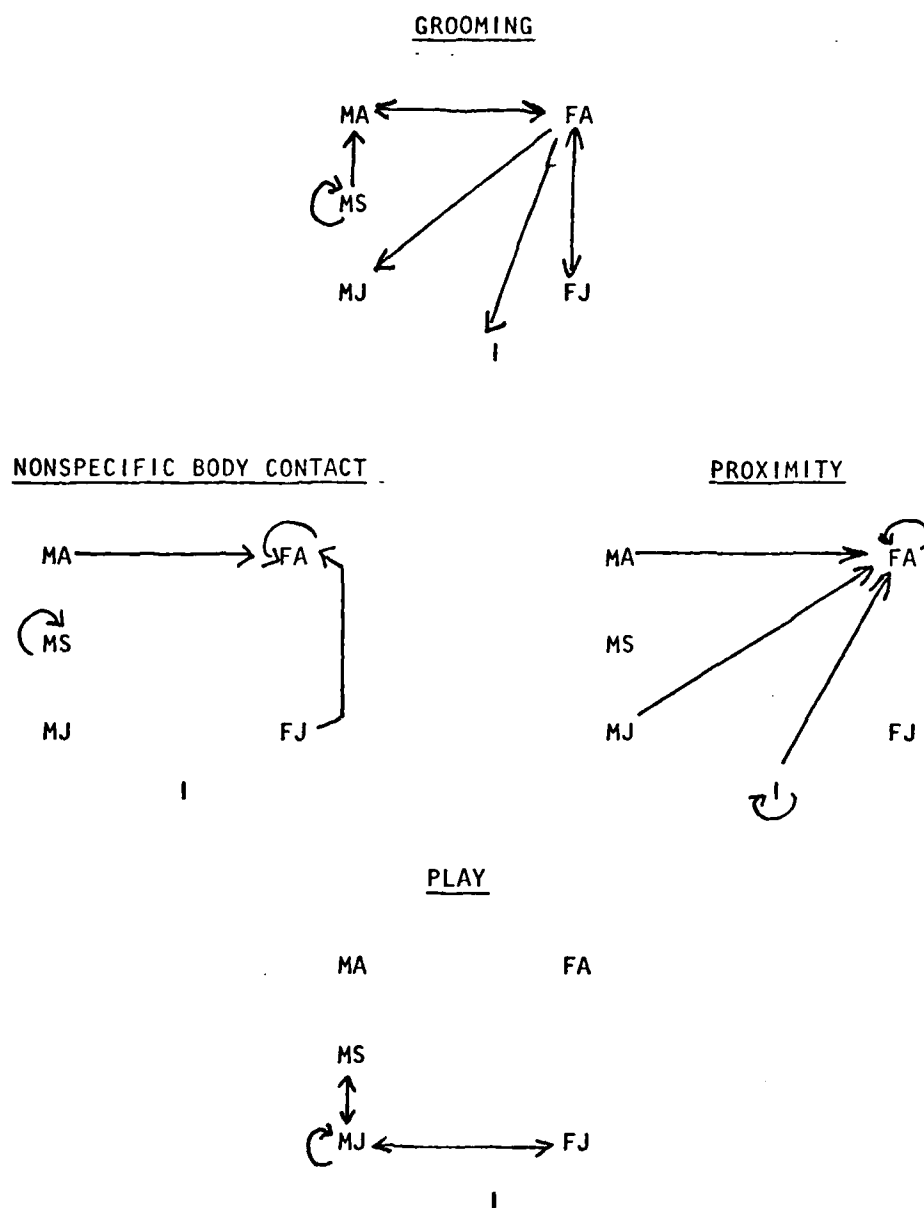
Figure 3. Typical interactions between ages/sex classes combined for T-
and NT-Troops. Arrows show direction of the interactions.
Criteria for drawing an arrow were based on pairwise comparison
tests of time spent in each activity. M, male; F, female; A, adult;
S, subadult; J, Juvenile; I, Infant. From Perkins, 1981.

GROOMING

NONSPECIFIC BODY CONTACT

PROXIMITY

PLAY

Figure 3. Typical interactions between ages/sex classes combined for T-
and NT-Troops. Arrows show direction of the interactions.
Criteria for drawing an arrow were based on pairwise comparison
tests of time spent in each activity. M, male; F, female; A, adult;
S, subadult; J, Juvenile; I, Infant. From Perkins, 1981.

In T-Troop, where Perkins found a lot of intermale affiliative behavior between July and November, the correlation between male rank and the frequency of social behavior between adult males was +.94 for the period April through July, but only +.34 from mid September through November. When we looked at the period when Knees was absent from T-Troop -- early August through mid . September, the correlation was still high (+.90, n=5). On the day of Knees' return, there was very little aggression, but a relatively high amount of intermale nonagonistic social behavior with Knees as the focus of this activity. For the last two weeks of September, there was nearly three times as much intermale social activity per observation period as there was from April through July; the high rate continued at about twice normal levels through October, and approached premanipulation levels during November. During the six weeks following Knees return, then, there was a high frequency of inter-male nonagonistic, nonsexual behavior on the part of all of the adult males and this eliminated the correlation between social rank and this class of behavior in these animals. As the rate of other social behavior among males dropped toward more normal levels in November, the correlation reappeared and reached +.81 for the 10 days of observations recorded in November, 1980. In cases where the positive relationship between high rank and high frequency of other social behavior was found, the higher the rank of the male, the more social behavior he received from the males of lower rank. Intermediate ranking animals tended to do and to receive approximately equal amounts of social behavior, while low ranking animals tended to do more and receive less. (The low ranking animals also tended to a lower total level of this activity).

In NT-Troop, the correlation between intermale social behavior and male rank was only +.63 for April-July and +.54 from August-November. It will be recalled from the Perkins study that there was about 4 times more aggression in NT-Troop than in T-Troop during the summer and fall of 1980. When the data were examined month by month, it was found that the April data, which were obtained after the NT-Troop males were placed back in the troop after an absence of six weeks, looked very much like that seen in T-Troop after Knees' reintroduction in September. That is, there was a high frequency of social behavior among all of the animals. While the top three animals in the hierarchy were involved in two to three times as much intermale social activity as four of the other five adult males, the resulting correlation of +.67 was not significant. Subsequently, the amount of intermale social behavior declined, but the correlations did not improve. Instead, the amount and direction of the intermale social behavior appeared to reflect agonistic alliances between pairs of males. This also appeared to be the case during August through November, following the removal of Quotation from the Troop, when aggression was high and intermale social interactions declined in freuqency.

In summary, there is a positive relationship between nonagonistic, nonsexual (affiliative) social behaviors and the social rank of adult male fascicularis monkeys. This relationship can be accounted for, in part, by the sexual behavior and opportunities of the adult males. In general, the higher the rank of a male, the more opportunity he has to engage in copulatory behavior and the more sexual behavior he exhibits. This appears to account for increased grooming, approaching, and physical proximity observed in copulating pairs and contained within the "other" social category of behavior.

The presence of this correlation, while of some interest in itself, does not contribute much to an understanding of those aspects of social organization and behavior as may be involved in the relationship between social behavior and laboratory performance. On the other hand, both the amount of intermale social behavior and the presence or absence of a relationship between rank and nonagonistic, nonsexual behavior among adult males do appear to be related to levels of aggression and to the social dynamics of the male social hierarchy. As such, they may be helpful in determining the amount of social tension within the groups and in predicting relationships between performance and social status. Finally, although kinship relationships appear to be important in relation to the social organization of females and juveniles within a troop; their role in influencing the organization of the male hierarchy is probably secondary to variables involving intermale aggression, intermale nonagonistic alliances, and sexual factors. It now seems to us that the transition from subadult male to adult and the subsequent integration into the dominance hierarchy is the critical step for the social development of the male and that this procedes in a manner which is largely independent of maternal influence, even though the mother continues to exhibit affiliative behavior toward her subadult and adult sons.

Conclusions and Recommendations

The experiments and observational studies conducted during the project have shown that there are relationships between social variables and performance on laboratory tests of learning and performance. The findings may be briefly summarized:

1. Response bursting following omission of reinforcement was observed in both rhesus and fascicularis monkeys. High levels of bursting were associated with high rank in the male dominance hierarchy in rhesus when the animals were tested on a fixed interval (FI) operant schedule. This relationship did not appear when the fascicularis were tested on this schedule. The reason for the species difference appeared to be the different ways in which the species handled the contingencies of the FI schedule. High ranking rhesus tended to have low response rates under 100% reinforcement whereas high ranking fascicularis tended to have high rates under the same condition. As a result, the relationships between response rates and the omission ratios (R_0) used to measure bursting were quite different in the two species. However, when omission of reinforcement was presented to fascicularis while they were working on a random interval schedule in a situation designed to maximize frustration, the relationship between rank and bursting did appear. It was most apparent when there was considerable agonistic interaction in the group and during periods when the male rank structure was changing.

2. Response bursting occurred in fascicularis working on differential reinforcement of low rate (DRL) schedules when animals failed to delay long enough to obtain a reward. High levels of bursting were associated with high levels of aggressive behavior in the social group and, less reliably, with high social rank in the dominance hierarchy. (Rhesus monkeys were not available for testing on this, or any other of the tasks mentioned below.)

3. High ranking fascicularis made more errors on reversal problems than low ranking animals. This was true for both a visual discrimination reversal task and an object quality reversal task. In the object quality task, performance varied directly as a function of rank. The same animal tended to perform worse when it rose in rank and better when it fell. Analysis of the response patterns of the animals did not reveal any relationships between response strategies and social variables. High ranking animals did not perseverate incorrect responses any more than did low ranking animals.

4. High ranking fascicularis tended to do more poorly than low ranking animals in learning object quality discrimination habits, but did as well as low ranking animals on measures on concept formation in the object quality learning set situation. High ranking monkeys did somewhat better than low ranking animals during acquisition of efficient performance on both DRL schedules and changeover ratio schedules.

5. Although high ranking monkeys entered a strange environment more readily than low ranking animals in an open field test, the relationship was transient and, perhaps, fortuitous, since changes in social rank were not accompanied by changes in emergence latencies on subsequent tests. There were no relationships between responses to novel objects or social stimuli in the open field and social variables derived from observations of the monkeys in their social groups.

Thus, there was little or no support for the idea that there might be a trait, or constellation of traits, which predisposes a particular monkey to both certain kinds of social behavior and certain kinds of performance. During acquisition, high ranking animals did better than low ranking animals on some tasks and worse on others. Better performance on the acquisition of difficult schedules such as the DRL with a limited hold contingency and the changeover ratio task suggest there may be a relationship between intelligence and tendencies to high social status. However, the disruptions of performance evidenced by response bursting and reversal errors in the higher ranking and more aggressive animals suggest that the most important relationships between social variables and performance involve something other than learning ability. In addition, the open field tests did not produce any relationships between social variables and individual differences relating to emotionality or curiosity.

Furthermore, observations of social behavior made immediately following laboratory testing did not reveal any relationships between daily performance and social behavior. There was no evidence that the consequences of an individual monkey's good or poor performance on a given day carried over to the social situation and altered its social behavior in any predictable fashion.

Instead, it appeared that the effects of social encounters carried over to certain aspects of performance on the laboratory tasks. The most important of these were not daily effects, but were relatively long term, suggesting that there was something about the general social situation of the individual animals that produced a state in the animal that was reflected by response bursting and difficulties with the reversal learning problems. The social variable most often related to performance was social rank within the male dominance hierarchy. These relationships were strongest during periods when the hierarchy was under tension -- when changes in rank were occurring and/ or when agonistic behavior increased, either spontaneously or as a consequence of the removal or replacement of key males.

A hypothesis involving a concept of social stress could account for the relationships seen in our animals. The hypothesis says that the establishment and maintenance of a particular position within a male dominance hierarchy places the animal under a certain amount of stress. The amount of stress would be expected to vary depending upon the social situation -- the degree of agonistic behavior exhibited by other males, the presence or absence of affiliative alliances, etc., but the achievement of high rank or the maintenance of high rank in the face of challenges to that rank might result in maximum social stress on that animal. Under high stress, the changes in task contingencies and requirements involving omission of reinforcement and reversals of previously correct stimuli might lead to excessive response bursting and poorer performance on reversal learning. Subadults and low ranking adult males that are not involved, or are involved only marginally, in the maintenance of the male rank structure would be under little social stress and would

exhibit little or no disruption of performance. It might also be hypothesized that there is a "U" shaped function relating social stress to performance such that, at moderate levels of stress, performance might be better than it is at either high or low levels. We would then predict a relationship in which amount of stress, task difficulty, and task contingencies would interact and, under some circumstances, high ranking animals could be expected to do better than low ranking animals.

To account for all of the data in these terms, it is necessary to introduce another idea. Animals which were defeated in social interactions which took place during the time performance testing was in progress often showed moderate to severe depressions in performance. This too, could be a stress effect, but it appears to be more closely related to the nature and severity of individual animal's defeat than to its status in the group or the dynamics of the male dominance hierarchy. Generally, it was an acute effect, lasting from a few days to two or three weeks.

Thus, the conclusions of this project are contained in the hypothesis that social variables and performance are related to each other through social stress which alters performance. To test experimental questions arising from this hypothesis, we would recommend that:

1. An independent measure of social stress should be obtained. Because social status is the product of many factors, and because increased or decreased social tension between individuals or within the hierarchy may not always be expressed in overt changes in agonistic behavior, it is suggested that plasma hormone assays be used to obtain an index of social stress. Corticosterone and testosterone have been shown to relate to stress and social status, respectively, and prolactin, which increases in direct relationship to the amount and intensity of physical stress in rodents, would be a prime candidate for use in this effort.

2. The best task for assessing performance changes at the present time are the DRL schedule with a limited hold and the random interval schedule with omission of reinforcement. Although the WGTA tests on reversal problems produced a strong relationship between performance and social rank, the tasks are very time consuming and expensive in terms of manpower. It is also more difficult to do repeated tests on the same task with the same animals, after they have undergone changes in social status between tests. Our early hopes that extinguishing the object quality reversal set would "erase" all of the previous learning and make retesting more feasible were not completely borne out. A promising possibility would be the use of multiple schedules which would allow for measuring "behavioral contrast" effects as a function of stress and social variables. We had intended to investigate the effect of both MULT VI-VI extinction and MULT DRL-VI schedules during the last year of the contract, but encountered serious difficulties with the software needed to run these tasks and were unable to meet this objective before the project expired. We also did some pilot work in which manipulanda were placed in the animal's compounds so that they could be tested on operant tasks in the social group situation. This paradigm deserves further study.

3. Although the social behavior of adult male fascicularis is somewhat different in all male groups than it is in groups composed of naturally occurring combinations of all age/sex classes, the key to the relationships between

performance and social variables appears to be the adult male dominance hierarchy. Although the matriarchical structure of the group is important, particularly in the establishment of affiliative bonds between individuals, it does not seem to play a critical role in the establishment or maintenance of the adult male hierarchy. As a result, it would appear that future investigations of social and performance relations can safely use all male groups and concentrate on the male hierarchy when using breeding groups. One question of interest, however, would involve the *study of performance* over time by *young* males as they reach adulthood and become involved in the social dynamics of the male hierarchy.

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